A TREATISE

ON

HUMAN PHYSIOLOGY;

DESIGNED FOR THE USE OF

STUDENTS AND PRACTITIONERS OF MEDICINE.

BY

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TO MY FATHER,

JOHN C. DALTON, M.D.,

IN

HOMAGE OF HIS LONG AND SUCCESSFUL DEVOTION

TO THE

SCIENCE AND ART OF MEDICINE,

AND IN

GRATEFUL RECOLLECTION OF HIS PROFESSIONAL PRECEPTS AND EXAMPLE,

This Volume

IS RESPECTFULLY AND AFFECTIONATELY

INSCRIBED.

PREFACE.

SINCE the last edition of this work, nearly all the departments of medicine have been cultivated with marked success; and the advances in physiological science during that time have made it desirable to revise the greater part of the book, and, in some respects, to modify its arrangement. In the section of Physiological Chemistry, the most important alterations relate to the classification of the Albumenoid Substances, and particularly to the prominence given to the Ferments as a special group. Although we are still very imperfectly acquainted with the chemical constitution of these bodies, and are even able to recognize them rather by the effects which they produce than by their physical properties, yet their physiological activity has assumed an importance which makes it necessary to consider them by themselves. In treatises exclusively devoted to Physiological Chemistry, the albumenoid substances are usually classified according to their characters of solubility in neutral, acid, or alkaline media, or in saline solutions of different degrees of concentration, or by the varying conditions of their coagulability; but in a work like the present, an arrangement based on their physiological properties and destination is both more useful and more intelligible. The same remark will apply, in great measure, to the other principal groups of organic substances.

In the department of the Nervous System, more extended consideration has been given to the localization of function in special parts of the cerebro-spinal axis. The recent progress of investigation in this respect relates not only to the cerebral convolutions and their connection with various forms of movement and sensation, but also to the identification of special communicating tracts of white substance in the brain and spinal cord. The general use of hardened and stained preparations, and improved methods in making microscopic sections, have largely increased our knowledge of the intimate structure of the nervous centres; and the study of nervous degenerations has proved an additional source of information in regard to their deep-seated connections. Although the anatomical data obtained in this way must be insufficient by themselves to determine the functions of a part, yet they are of material aid in the contrivance and execution of physiological experiments, and often indispensable for the explanation of their results. Furthermore, the study of the vaso-motor nerves and nerve centres has reached a development which makes it almost a special department of nervous physiology, and requires a more extended treatment than heretofore.

The method of examination by microscopic sections has also been found of advantage in Embryology. It shows the form and position of the organs at their earliest period of development, and enables the observer to trace their subsequent changes with greater precision than formerly. The most primitive embryonic structures are still those which present the greatest difficulty in their study and interpretation; but increased facilities of research are constantly adding to our knowledge in this respect, and reducing the number of doubtful or disputed points. In the present work, as a general rule, topics which are uncertain or incomplete have been treated with comparative brevity, a greater space being devoted to those which are demonstrated by satisfactory evidence. The number of wood-cuts has been somewhat reduced, and many have been replaced by new ones, intended either for the illustration of recent discoveries or as improvements on those of the former edition.

New York, *December*, 1881.

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ACCORDING TO THE METRIC SYSTEM, EMPLOYED IN THIS BOOK.

One gramme . . . . = 15.434 grains.
One kilogramme (1000 grammes) = 2.2 pounds Avoirdupois.

One micromillimetre . . . . = 0.00004 ($\frac{1}{25000}$) inch.
One millimetre . . . . = 0.0394 ($\frac{1}{25}$) “
One centimetre . . . . = 0.394 ($\frac{4}{10}$) “

One cubic centimetre . . . . = 0.061 cubic inch.
One litre (1000 c. c.) . . . . = 61 cubic inches (0.035 cubic foot).

HUMAN PHYSIOLOGY.

INTRODUCTION.

PHYSIOLOGY is the study of the phenomena of life. It makes us acquainted with their immediate causes, the conditions of their manifestation, the material changes in the body by which they are accompanied, their mechanism, and their results. It teaches us all that can be known of the living organism in a state of activity, with its different parts performing their appropriate functions, and the whole structure exhibiting the characters of individuality and life.

In physiology, as in all the other natural sciences, direct observation is the only means by which actual knowledge can be attained. Ample experience has demonstrated that in these departments analogical deductions and inferences are unsafe, and that every question must be tested by experimental investigation. Even the anatomical structure of an organ can never indicate with certainty its physiological properties, until by immediate examination we have found the function to be associated with the structure. This method, which depends entirely upon observation, is laborious and difficult; but it is the method to which we owe all our present knowledge of natural phenomena, and the only one which can produce similar results in the future. There are some special considerations regarding its application to physiology, owing to the intricate constitution of organized beings, and the complexity of their functions.

The entire body is a composite structure, made up of many parts with varied characters and properties; and the life of the organism as a whole depends on the combined activity of its different parts. Consequently each one of these should be first studied by itself, in order to ascertain, so far as possible, its individual characters. This may be done in great measure by the examination of single parts, separated from the rest; because minute anatomical structures, like muscular fibres or nerve fibres, owe their distinguishing properties directly to the nature and combination of their constituent materials. So long as they are connected with the living organism, their physical constitution is maintained by the supply of nutriment from the blood and interstitial fluids. But after this supply is cut off, they still remain for a time sufficiently unaltered to exhibit their specific characters. By this means we learn that the physiological property of a muscular fibre is contractility; and that there are two kinds of these fibres, the striped and the unstriped, both of which contract under the application of a stimulus, but with different degrees of rapidity. A nerve fibre, on the other hand, has the power of transmitting a stimulus to distant regions, and of calling into activity other parts with which it is connected. In certain instances the action and products of special glandular tissues may be studied with some success in a similar way. As a general rule, investigations of this kind are most readily carried out in the cold-blooded animals; because their tissues are the seat of a less rapid alteration than in the warm-blooded classes, and retain their normal properties for a longer time after separation from the body.

But the functional activity of entire organs, or of an apparatus of associated organs, can be studied only by experimental observation upon the living body. A compound structure produces results in which all its various parts have their share, and which are affected by the manner in which these parts are combined in successive or simultaneous action. Thus every muscular fibre in the walls of the heart has the same simple property of contractility; but the physical action of the organ, as a whole, is produced by so many contractile fibres, arranged in so complex a form, that it needs a direct inspection of the living heart to show the character, rhythm, and frequency of its pulsations. The glandular organs yield secretions which contain not only the special products of their cells, but also materials supplied from the circulating blood; and this supply varies in quantity and composition according to different nervous and vascular conditions. In the digestive apparatus a number of secretions act, in succession or together, upon the elements of the food, and thus modify the properties derived from their individual composition. These facts make it necessary, in the solution of the most important questions, to study the animal functions by means of observation and experiment during life.

The progress of physiology at the present day is characterized by the general adoption of methods which yield results in many respects more definite and positive than those formerly attained. This is largely due to the improvements in physics and chemistry, which place at the disposal of the physiologist more effective means of investigation. Many of the phenomena presented by living bodies can now be examined, measured, and recorded by the aid of optical, electrical, photographic and registering instruments, by which our knowledge in regard to them is rendered both more extensive and more precise. We are also enabled by this means to compare the results of different observations, and to reach the important deductions based on the relation of quantities. This seems to be still the most imperfect department of the subject, and one in which we are most liable to hasty conclusions from insufficient data; but the method is one of great promise, and has already produced much certain and useful information. The animal functions are examined in every way in which they are accessible to physical and numerical investigation. The structure of each organ, and the constituent materials of its tissues, are determined by appropriate means. The changes in its volume, temperature, vascularity, and composition, the nature and quantity of the materials consumed and of the force manifested, are ascertained and registered. The new substances produced are tested and measured, and the accompanying changes in other organs, or in the whole body, are subjected to similar examination.

In this way the physiologist studies the living body as a machine. He endeavors to learn the construction of its parts, the mechanism of their action, the materials with which it is supplied, the chemical transformations of its internal nutrition, and the phenomena which it exhibits in every department of the vital operations. For this purpose he employs all the available means of scientific investigation.

A large part of the phenomena presented by living creatures are general in character, and show themselves in all classes of vegetable and animal organisms. The absorption of new material and the discharge of waste products, indicating the incessant renovation of the organized fabric, and the direct relation between the quantity of nutriment consumed and the active manifestation of vitality, are noticeable facts in every form of animated existence. Some of the materials and conditions necessary to life are the same in all cases. The consumption of oxygen and the discharge of carbonic acid are universal phenomena, both in animals and vegetables. The presence and absorption of moisture are also indispensable conditions; and in every case there are certain limits of temperature which cannot be overpassed in either direction without disturbance or arrest of the vital operations. The general nature of these conditions shows their fundamental importance in the phenomena of life, and requires a certain acquaintance with vegetable physiology as an aid to the more successful study of the animal functions.

On the other hand, there are some special forms of vital activity which are confined to vegetables, and others which are met with only in animals. Thus, the deoxidation of carbonic acid and water, together with the combination of their remaining elements to form organic materials, can be accomplished only by the living tissues of green vegetables; animals having no power to produce organic matter, but only to consume it. Furthermore, it is only in the higher animals that consciousness, sensation, and volition appear to have a distinct existence, and come into prominence in connection with the functions of the nervous system. In the animal kingdom certain materials or modes of activity are so nearly the same in many different classes as to indicate a close relation with some common feature of their organization; while others, on the contrary, are confined to two or three species alone. Thus, the red coloring matter of the blood is identical in color, general composition, optical properties, and physiological action throughout the different groups of quadrupeds, birds, reptiles, and fish; in all of them the nerve fibres have the same distinctive endowments of motor and sensitive qualities, and the internal reactions are performed by the nerve centres in a similar way. But the power of producing electric shocks exists only in a few species of fish, which resemble in all other respects the fishes which are non-electric. Both the general nature of the more common functions, and the specific character of those which are exceptional, become legitimate sources of knowledge in physiological science.

The physiology of the human species includes all the more general and fundamental facts common to man and animals, as well as the specific differences peculiar to the human organism. These differences, as a general rule, do not relate to the character of the vital phenomena nor to their mode of production, but only to their quantity or intensity. Thus the animal heat, produced in the living tissues, is generated no doubt by processes of the same kind in the human species as in quadrupeds; but the exact temperature of the human body, and its normal variations, are to be determined by direct observation upon man. The consumption of oxygen and the exhalation of carbonic acid take place in essentially the same manner in man as in the higher animals; but the precise quantity of each, and their numerical relation to other ingredients or products of the body, are peculiar to man and must be ascertained by special examination. Nearly all the observations, therefore, requiring to be made upon the human subject, relate to matters of detail, most of the general and fundamental facts being reached by investigations in the physiology of animals. The exceptions to this rule are mainly connected with certain functions of the nervous system, which are so highly developed in man, as compared with the animals, that their activity becomes different in kind as well as in degree. Thus the faculty of articulate language, which has no existence in animals, has been localized in a particular region of the brain, wholly by means of observations upon man; and it is probable that the same methods will be requisite in regard to some other of the nervous functions. But in most respects the phenomena of human physiology are intimately connected with those of the higher animals.

The study of physiology is naturally divided into several departments or sections, each of which deals with certain special subjects, and is distinguished by the nature of the facts investigated, the methods by which they are examined, and their relation to the vital activity of the whole body.

The first section is devoted to *Physiological Chemistry*. It comprises the study of the chemical ingredients of the living body, their composition and reactions, the source from which they are derived, their quantity and distribution in the animal frame, their occurrence as constituent parts of the food, their combinations and decompositions in the body, and the form under which they appear in the products of excretion. It aims to give a general view of the materials supplied to the animal organism, and the use which they subserve in the processes of life.

The second section treats of the functions of *Nutrition*. It includes the action of the digestive apparatus, by which the food is prepared for assimilation, the absorption of the digested products, their elaboration in the glandular organs, the blood and its circulation, the formation and character of the secretions, the phenomena of respiration, the production of animal heat, and the constitution and properties of the excreted fluids. These processes have for their object the vegetative growth and renovation of the body, or the maintenance of its normal structure and organization. They are for the most part of a physical or chemical nature, and are distinguished from other physical or chemical phenomena only by the variety and complexity of their results.

The third division in the natural order of study embraces the functions of the *Nervous System*. These functions are of a different character from the preceding, and are investigated by different means. The two groups of phenomena are thus distinguished from each other, notwithstanding the fact that they are mutually dependent. The activity of the nervous system requires for its support a continued nutrition; and on the other hand the influence of the nervous system is everywhere felt by the organs of circulation and secretion. But the immediate action of the nervous system is, so far as we can judge, of a special nature, and one which has no resemblance to the nutritive operations. It is a means of sympathetic communication, by which the different organs are alternately stimulated or controlled, and which acts as the instrument of sensibility, consciousness, volition, and movement. It brings the living body into active relation with the external world, and provides for the exercise of the animal instincts and powers.

The last group of functions contains those belonging to *Reproduction*. They are made up of phenomena, different in kind from either of the foregoing, and having for their object the continuation of the species. They consist in the production, from the parent organism, of the sexual elements, and in the appearance, from the union of these elements, of a progressive series of organic forms, following each other in a determinate order of successive transformations, until the last form in the series reproduces that of the original parent. The distinguishing feature of this process is therefore that the functions of nutrition and growth are here directed by a law of continuous development; and it presents, as the main object of our study, the form and structure of the different parts as they successively appear in the growing organism.

SECTION I.

PHYSIOLOGICAL CHEMISTRY.

CHAPTER I.

CHEMICAL INGREDIENTS OF THE BODY.

THE first requisite, in the study of the vital operations, is a knowledge of the substances which make up the animal frame. It is these substances which give to the organic tissues and fluids their specific character; and the manner in which they are supplied, and the changes which they undergo within the body, constitute the basis of all the properties which distinguish the living structure.

If we examine any one of the fluids contained in various parts of the body, such as the blood, the lymph, the bile or the saliva, we find that it is made up of a number of different ingredients, mingled together in certain proportions. Thus the blood contains albuminous matters and water, together with calcareous or alkaline chlorides, carbonates, and phosphates. In the bile there are biliary salts, coloring matters, cholesterine, and mineral substances; and the saliva is a mixed solution of albuminous and saline ingredients. The proportion of these ingredients, in each animal fluid, is maintained by the process of nutrition at about the same standard; those which are expended and lost in the vital operations being replaced by others of the same kind derived from the food or produced by the transformation of other materials.

There is a similar association of different ingredients in the solid parts of the body. Even where the animal tissue appears most homogeneous, it contains a variety of materials, and it is probable that the minutest fibre or membrane in the system is made up in the same way of several constituents. In the hard substance of bone, for example, there is water, which may be expelled by evaporation; lime phosphate and carbonate, which may be extracted by solvents; a peculiar animal matter, with which the calcareous salts are in union; and various other saline substances, in special proportions. The muscular tissue contains water, sodium and potassium chlorides, lime phosphate, creatine, albumen, coloring matter, and myosine. It is the object of physiological chemistry to isolate these different substances from each other, to study their specific properties, and to learn the part taken by each in the act of nutrition.

But it is very important in this investigation to determine what are the real ingredients of the animal frame, and to distinguish them from the abnormal products of their change or decomposition. The substances in question must be extracted from the tissues and fluids of the body by the aid of physical and chemical manipulations, such as evaporation, solution, precipitation, and crystallization. Many of them are of a nature to be altered or decomposed by the treatment to which they are subjected, or even by the unnatural conditions resulting from the cessation of life. The coagulable substances of the blood and of the muscular tissue, which are fluid during life, soon after death pass into the solidified condition, and thus no longer present their original characters. The red coloring matter of the blood requires to be extracted at a temperature nearly as low as the freezing point of water, otherwise it loses its natural composition and becomes changed into other substances. The normal coloring matter of the retina is bleached by the action of daylight, and so disappears altogether unless special precautions be used for its protection. This sensibility of the organic ingredients, making them liable to be affected by unnatural conditions, is the reason why many of them have long remained unknown or misunderstood; and it also accounts in great measure for the changing nomenclature of physiological chemistry. By improved methods of extraction, an organic ingredient is often obtained in a new form, which more fully represents its normal character; and it therefore receives a different name, to distinguish it from the former substance. Thus, the coloring matter of the red blood-globules, formerly known as "hematine," was obtained from the blood in an insoluble condition by the use of heat and acids. Subsequently, when extracted by the simpler action of water and alcohol, at low temperatures, retaining its natural color, solubility, and spectroscopic character, it was named "hemoglobine," and was recognized as the real constituent of the red globules.

The physiological ingredients, therefore, of the animal frame are substances which exist in its solids or fluids under their own form, and are obtained by means which do not change them into other matters or decompose them into their chemical elements. Lime phosphate, for instance, is an immediate constituent of the bony tissue, but phosphoric acid is not so, for it is not present under its own form, but is obtained only by breaking up its combination with the calcareous matter; while phosphorus is a product of still further decomposition of the phosphoric acid. An animal substance containing the alkaline acetates or lactates, if treated by incimeration in the air, would yield as a residue the carbonates of the same bases, the original organic acids having been destroyed and replaced by carbonic acid. As a rule, accordingly, in the examination of animal tissues, the simplest forms of chemical manipulation are most successful. The substance or fluid is first subjected to evaporation, in order to extract and estimate its water. The evaporation is conducted at a heat not above 100° C, or the boiling point of water, since a higher temperature would often be injurious to the organic ingredients. From the dried residue sodium chloride, alkaline sulphates, carbonates, and phosphates are extracted with water. Coloring matters are usually separated by alcohol, and oils may be dissolved out by ether. When a chemical decomposition is unavoidable, it must be kept in sight and afterward corrected. Thus, the sodium glycocholate of the bile is separated from certain other ingredients by precipitating it with plumbic acetate, forming lead glycocholate; but this is afterward decomposed in turn by sodium carbonate, reproducing the original sodium glycocholate. Certain organic materials of peculiar physiological activity are extracted by means of glycerine, which preserves them indefinitely in an unaltered condition; and as a general rule the improvements in this branch of investigation consist in exact regulation of the temperature, the avoidance of strong acid and alkaline reagents, the employment of mild solvents and precipitating solutions, and in especial care that the substance to be examined is obtained in a fresh condition, unchanged by cadaveric alterations. By this means we may form a tolerably correct estimate of the nature, quantity, and properties of the constituent materials of the living organism.

The manner in which these ingredients are associated together is also deserving of notice. In every animal solid and fluid, there is a number of different substances present in certain proportions, so united with each other that the mixture presents a homogeneous appearance. But this union is of a complicated character; and the presence of each ingredient depends, to a certain extent, upon that of the others. Some of them, such as the alkaline carbonates and phosphates, are in direct solution in the water. Some, which are insoluble in water, are retained in solution by the presence of other soluble substances. Thus, the insoluble lime phosphate of the urine is held in solution by the acid sodium biphosphate, also present as an ingredient. In the alkaline blood-plasma, on the other hand, the lime phosphate is liquefied by union with the albumen, which is itself soluble in the water of the plasma. The same substance may be fluid in one part of the body, and solid in another part. Thus, in the blood and secretions the water is fluid, and holds other substances in solution; while in the bones and cartilages it is solid, by its union with the animal and saline ingredients, abundantly present in the solid form. In the blood, the lime phosphate is fluid by solution in the albumen; but in the bones it forms a solid substance with the animal matter of the osseous tissue; and the union of the two is as intimate and homogeneous in the bones as in the blood. An animal ingredient, therefore, never exists alone in any part of the body, but is always associated with a number of others, by homogeneous mixture or mutual solution.

The proportion in which each ingredient is present, in any animal solid or fluid, is, as a rule, characteristic of that tissue or secretion, and contributes largely to its physiological characters. Thus, water is present in large quantity in the perspiration and the saliva, but in small quantity in the bones and teeth. Sodium chloride is comparatively abundant in the blood and deficient in the muscles. On the other hand, potassium chloride is more abundant in the muscles, less so in the blood. But these proportions are nowhere absolute or invariable. There is a difference, in this respect, between the chemical composition of an inorganic substance and the physiological constitution of an animal fluid. The former is constant and definite; the latter always presents certain variations. Thus, water is invariably composed of the same relative quantities of hydrogen and oxygen; and these proportions are essential to its existence. But in the urine, the proportions of water, urea, urates, and phosphates vary within certain limits in different individuals, and even in the same individual, from one hour to another. This physiological variation takes place, within the limits of health, in all the animal solids and fluids. It is a necessary accompaniment of the actions of life, and one of the characteristic phenomena of living beings. The animal body is the seat of incessant changes, and all its manifestations of vital activity are either the causes or the result of its internal alterations. Every variation in its general condition is accompanied by a corresponding variation in the constitution of its different parts. This constitution is consequently of a very different character from the chemical constitution of an oxide or a salt. In the analysis of an animal tissue or fluid, the numbers expressing the proportion of its different ingredients are always understood to be approximate, and not absolute. They represent the general character of the mixture, but allow of its variation within physiological limits.

The chemical ingredients of the body are naturally divided into five classes:

The first of these classes comprises all ingredients of a purely INORGANIC nature. These substances are derived mostly from the exterior. They are found abundantly in the inorganic world as well as in organized bodies; and they present themselves under the same form and with the same properties in the interior of the animal frame as elsewhere. They are crystallizable, with definite chemical characters and a simple chemical constitution. They are compounds, in simple proportions, of hydrogen and oxygen, the metals of the alkaline and earthy salts, sulphur, phosphorus, chlorine, and, in general terms, of the ingredients of mineral substances. They comprise water, which is the most abundant of its class in the animal frame, sodium and potassium chlorides, phosphates, and sulphates, alkaline carbonates, the salts of lime and magnesia, together with combinations of a few other metallic elements in small quantity.

The second class consists of the HYDROCARBONACEOUS SUBSTANCES of organic origin. They are distinguished from inorganic matters first by the fact of their containing *carbon* in large proportion as one of their immediate constituents, associated with hydrogen and oxygen, but with no other chemical element. They are either crystallizable or readily convertible into other crystallizable members of the same group. Their chemical composition is less simple than that of inorganic substances, but it is still sufficiently definite, and their chemical characters are well marked and easily recognizable. They first make their appearance in the interior of organized bodies, and are not found in the inorganic world, excepting as the remains or products of animal or vegetable life. To this group belong the several varieties of starch, sugar, and oil.

The third class comprises the ALBUMENOID or nitrogenous organic matters. These substances derive their name from the albumen or white of an egg, which was among the earliest to be studied, and which may be considered as a representative of the whole class. They differ from the substances of the two preceding groups, especially in the fact that they contain *nitrogen* as an ingredient, in addition to the three elements of the hydrocarbonaceous matters. They are exclusively of organic origin, appearing only as ingredients of the living body. Their chemical constitution is a complicated one—that is, their four elements are united in such a way as to form compounds of a very high atomic weight, which has not, however, been determined with sufficient precision to give an exact chemical formula. Their reactions with other substances are not well defined, as compared with the inorganic constituents, and their most striking physiological properties are not such as can be expressed in chemical phraseology. Nevertheless, they are of the first importance as ingredients of the organized frame, since they form the largest portion of its mass, and contribute directly to its most active phenomena. They include such substances as albumen, caseine, ptyaline, pepsine, and myosine.

The fourth class is composed of the COLORING MATTERS. These substances, upon which the different tints of the solids and fluids depend, are present, for the most part, in small quantity, the most abundant being the red coloring matter of the blood.

Lastly, in the fifth class are embraced a group of CRYSTALLIZABLE NITROGENOUS MATTERS, many, if not all, of which are derived from the physiological metamorphosis of albumenoid substances. They are found in some of the solid tissues, as the brain and nerves, in the secretions of the liver, and especially in the urine, where they represent the products of excretion.

CHAPTER II.

INORGANIC SUBSTANCES.

THE *inorganic* substances are present in the animal body in great variety. Some of them, such as water and the salts of lime, constitute a large proportion of the mass of the tissues and fluids in which they are found; others are in comparatively small quantity. Some of them are found in all regions of the body, while others are met with only in particular tissues or fluids; but there are hardly any which do not appear as constituents of several different parts. As their name implies, these substances exist abundantly in the inorganic world, and form a large part of the crust of the earth. But they are also essential constituents of the animal frame, and necessary ingredients of the food. No regimen would be capable of supporting life indefinitely which did not contain them in due proportion.

This group includes the following substances:

- Water;
- Sodium chloride;
- Sodium phosphate;
- Sodium biphosphate;
- Sodium sulphate;
- Sodium carbonate;
- Potassium chloride;
- Potassium phosphate;
- Potassium sulphate;
- Potassium carbonate;
- Lime phosphate;
- Lime carbonate;
- Magnesium phosphate;
- Magnesium carbonate.

Beside the substances above named there are found, as constant ingredients of the incombustible residue of various parts of the human body, iron, silica, and fluorine; but it is not certainly known in what form of combination these substances originally existed in the animal solids and fluids. Sometimes, but not always, there are indications of the presence, in minute quantity, of copper, manganese, and lead, also in unknown forms of combination.

The most important of the inorganic substances, considered in regard to their quantity and their part in the vital phenomena, are the following:

1. Water, H_2O.

Water is present in all the tissues and fluids of the body. It is abundant in the blood and secretions, where it is indispensable in order to give them the fluidity necessary to the performance of their functions. For it is by the blood and secretions that new substances are introduced into the body, and old ingredients discharged; and it is a necessary condition both of the introduction and discharge of solid substances that they assume, for the time being, a fluid form. Water is therefore an essential ingredient of the animal fluids, for it holds their ingredients in solution, and enables them to pass and repass through the animal frame.

But water is a constituent also of the solids. If a muscle or a cartilage be exposed to gentle heat in dry air, it loses water by evaporation, diminishes in bulk, and becomes dense and stiff. Even the bones and teeth lose water in this way, though in smaller quantity. In all the solid and semi-solid tissues, the water which they contain is useful by giving them the special consistency which is characteristic of them, and which would be lost without it. Thus a tendon, in its natural condition, is white, glistening, and opaque; and, though very strong, perfectly flexible. If its water be expelled by evaporation it becomes yellowish, shrivelled, semi-transparent, inflexible, and unfit for performing its mechanical functions. The same is true of the skin, the muscles, the cartilages, and the glands.

The following is a list, compiled by Robin and Verdeil from various observers, showing the proportion of water per thousand parts in different solids and fluids:

Quantity of Water in 1000 Parts in

Teeth	100	Bile	880
Bones	130	Milk	887
Cartilage	550	Pancreatic juice	900
Muscles	750	Urine	936
Ligaments	768	Lymph	960
Brain	789	Gastric juice	975
Blood	795	Perspiration	986
Synovial fluid	805	Saliva	995

According to the best calculations, water constitutes, in the human subject, about seventy per cent. of the entire bodily weight.

The water which thus forms part of the animal frame is derived mainly from without. It is taken in the form of drink, and is also abundant in various kinds of food. For no articles of food are taken in an absolutely dry state, but all contain more or less water, which may be expelled by evaporation. The quantity of water, therefore, daily taken into the system, cannot be ascertained by simply measuring the quantity of drink, but its proportion in the solid food must also be determined, and this quantity added to that taken in with the fluids. By measuring the fluid taken as drink, and calculating in addition its proportion in the solid food, we have found, in accordance with the results formerly obtained by Barral, that, for a healthy adult man, the average quantity of water introduced into the system is about 2000 grammes per day.

There is reason to believe that a certain quantity of water also makes its appearance within the body by the liberation of its elements from various organic combinations. This is shown by the fact that a considerable quantity of hydrogen is daily introduced into the system in the organic ingredients of the food, which is not wholly accounted for in the excretions. The most reliable estimates, in this respect, are as follows:

Average Daily Quantity of Hydrogen

Introduced in organic combinations with the food . . .	40 grammes.
Discharged " " " excretions . .	6 "
Residue unaccounted for	34 "

Thus not more than fifteen per cent. of the quantity introduced is discharged in the organic ingredients of the excretions. But hydrogen is not exhaled from the body in notable quantity in a free state, nor in any other form of inorganic combination except water. The intestinal gases contain habitually hydrogen and carburetted hydrogen in the proportion of about thirty-eight per cent. of their volume.* The absolute quantity of these gases in the normal condition has not been determined; but it is evidently quite insufficient to account for the missing hydrogen, 34 grammes of which would occupy, in the gaseous form, a space of 379 litres. The surplus hydrogen must therefore be discharged in the form of water or watery vapor. The estimates given above indicate that not far from 300 grammes of water are daily produced in the body in this way. One important class of the ingredients of the food, hereafter to be described, already contain hydrogen and oxygen in the relative quantities necessary to form water; and, when decomposed in the system, they may readily yield these elements in the required proportions.

Furthermore, although it has not yet been proved, in any particular case, that more water is discharged from the system than can be accounted for by that introduced, yet a comparison of the average results obtained by different observers always tends to show a surplus of water discharged, from 200 to 500 grammes over and above that introduced with the food and drink. The quantity of water, however, thus produced in the body is small in comparison with that introduced and discharged under its own form.

While in the interior of the living body, water is useful principally by its physical properties. It is the universal solvent for the ingredients of the animal fluids, holding them in solution either directly or by the aid of other substances which are themselves soluble. It thus enables the elements of the food to find their way into the circulating fluid, and into substance of the organs. It permeates the membranes and brings into contact with each other the inorganic and organic materials of various parts, and enables them to assume new forms by mutual reaction. In this way it is subservient to the phenomena of absorption, transudation, exhalation, chemical union and decomposition, which make up the nutritive functions of the animal frame.

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* Marchand: Journal für praktische Chemie. Leipzig, 1848. Band XLIV., p. 10. Rüge: Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Wien, 1862. Band XLIV., p. 739.

After forming part of the animal solids and fluids, and taking its share in the vital processes, the water is again discharged; for its presence in the body, like that of all the other ingredients, is not permanent, but temporary. It makes its exit from the body by four different passages, namely, as a liquid in the urine and feces, and in the form of vapor by the lungs and skin. The quantity expelled in each case is not uniform, but varies according to circumstances. If the kidneys be unusually active, the watery ingredients of the urine are increased in quantity, while the cutaneous perspiration is diminished; and the state of the atmosphere and the rapidity of respiration will influence the amount of watery vapor exhaled by the lungs and skin. Still there is a well-marked average relation between the activity of the various organs and the quantity of their excreted fluids. It appears from a comparison of the researches of Lavoisier and Seguin, Valentin, and other observers, that the water discharged from the system passes by these different routes nearly in the following proportions:

By exhalation from the lungs	20 per cent.
By the cutaneous perspiration	30 "
By the urine and feces	50 "

While only four per cent. of the water is expelled with the feces, ninety-six per cent. passes out by the lungs, the skin, and the kidneys. It is evident, therefore, that the main bulk of the water taken in with the food does not simply pass through the alimentary canal, but enters the circulation, and becomes a temporary constituent of the solid tissues. As it appears in the secretions it brings with it various ingredients absorbed from the glandular organs; and when finally discharged it is mingled, in the urine and feces with salts and excrementitious matters, and in the cutaneous and pulmonary exhalations with animal vapors and odoriferous material of various kinds. In the perspiration it contains mineral sulphates and chlorides, which it leaves behind on evaporation.

2. Lime Phosphate, $2(PO_4)Ca_3$.

This substance exists as an ingredient in all the animal solids and fluids. So far as regards its mass, it is, next to water, the most important of the inorganic constituents of the body, its entire quantity being much greater than that of any other mineral salt. For though not especially abundant in the fluids and the softer tissues, it forms more than one-half the substance of the bones. It is estimated by Barral that the osseous tissues constitute 6.4 per cent. of the entire mass of the body; and lime phosphate forms on the average from 57 to 58 per cent. of the substance of the bones. This would give, for a man weighing 65 kilogrammes, or 143 pounds avoirdupois, 2400 grammes of calcareous phosphate in the whole body. Its proportion in various tissues and fluids of the human system is as follows:

Quantity of Lime Phosphate in 1000 Parts in the

Enamel of the teeth	885	Milk	2.72
Dentine	643	Blood	0.30
Bone	576	Bile	0.92
Cartilage	40	Urine	0.75

Notwithstanding the large quantity of lime phosphate in the body as a whole, it is evident, from the preceding list, that most of it is deposited in the solid tissues; while it is present in but slender proportion in the animal fluids. Of these fluids, milk alone contains lime phosphate in notable quantity, where it is plainly subservient to the ossification of the growing bones of the infant, by whom the milk is used as food. In the circulating fluids, the internal secretions, and the urine, on the other hand, the calcareous salt is in small amount. Its importance in the body depends mainly upon its physical property of imparting rigidity to the solid tissues, rather than upon its active qualities in the phenomena of nutrition.

In the solid tissues it is associated with other earthy and alkaline salts, but largely preponderates over them in amount. In the bones, the quantity of lime phosphate is from five to six times greater than that of all the other mineral ingredients together.

In the bones, teeth, and cartilages, lime phosphate exists in a solid form; not deposited mechanically as a granular powder, but united with the animal matter of the tissues, like coloring matter in colored glass, the union of the two forming a homogeneous material. It is not, on the other hand, so combined with the animal matter as to lose its identity and constitute a new substance, as where hydrogen combines with oxygen to form water; but rather as salt unites with water in a saline solution, both substances retaining their original character and composition, though too intimately associated to be separated by mechanical means. The lime phosphate, therefore, may be extracted by maceration in dilute muriatic acid, leaving behind the animal substance, which still retains the original form of the bone or cartilage.

In the solid tissues, lime phosphate is useful by giving to them their due consistence and solidity. In the enamel of the teeth, the hardest tissue of the body, it predominates exceedingly over the animal matter, and is present in greater proportion than in any other part of the frame. In the dentine it is in somewhat smaller quantity, and in the bones smaller still; though in the bones it continues to form more than one-half their entire mass. The importance of this substance, in communicating to bones their natural stiffness and consistency, is shown by the alteration which they suffer from its removal. If a long bone be macerated in dilute muriatic acid, the earthy matter is dissolved out, the bone loses its rigidity, and may be bent or twisted in any direction without breaking. (Fig. 1.)

In the formation of the bony skeleton during fœtal life, infancy, and childhood, the cartilaginous substance previously existing is replaced by osseous matter, which contains a larger proportion of calcareous salts; while the anatomical texture of the parts is also changed, giving rise to the characteristic forms of bony tissue. This progressive consolidation of the skeleton is known as the process of "ossification." In some instances it is defective, owing to partial failure in the powers of assimilation; and as the rigidity of the skeleton does not increase in proportion to the weight of the body and the force of muscular action, the bones become gradually bent and deformed, sometimes to an extraordinary degree. This affection has received the name of *Rachitis.*

Fig. 1.

Fibula tied in a knot, after maceration in a dilute acid. From a specimen preserved in spirit.

A similar result is produced by a morbid softening of the bones, sometimes occurring in adult life, known as *Osteomalakia.* In this disease the bony fabric, after its formation, becomes altered in texture and composition, and, the new substance which takes its place being deficient in calcareous matter, there is a progressive yielding and deformity of the skeleton, like that which happens in rachitis.

In the plasma of the blood the lime phosphate, though insoluble in alkaline watery liquids, is held in solution by union with the albuminous ingredients. It has been shown by Fokker that the earthy phosphates added to white of egg unite with the albuminous matter and become soluble in considerable proportion. This explains the presence of lime phosphate in a liquid form in the blood and in the milk, both fluids with an alkaline reaction. In the urine, on the other hand, it is held in solution by the acid sodium biphosphate. Accordingly, when the urine is rendered alkaline by the addition of soda or potassa, the earthy phosphates are precipitated, forming a white turbidity.

The source of the lime phosphate of the animal solids and fluids is in the food. It exists in nearly every animal and vegetable alimentary matter in common use. It is found not only in muscular flesh, eggs, and milk, and in all the cereal grains, as wheat, rye, oats, barley, maize, and rice, but also in peas and beans, the nutritive tubers and roots, as potatoes, beets, turnips, and carrots, and even in juicy fruits, such as the apple, pear, plum, and cherry.

After forming for a time a constituent part of the body, the lime phosphate is discharged with the excretions, but slowly and in small amount. According to the observations of Neubauer and Beneke, about 0.4 gramme, on the average, is daily expelled with the urine. A slightly larger quantity is found in the feces, but this may be only a residue from the undigested portion of the food. Only traces of it are to be detected in the perspiration. As so large a quantity of this salt, therefore, is contained in the body, while so little is expelled daily with the excretions, it is evidently one of the more permanent constituents of the frame; comparatively inactive in the process of internal metamorphosis, and serving for the most part as a physical ingredient of the solid tissues.

3. Lime Carbonate, CO_3Ca.

Lime carbonate is found in the bones, the teeth, the blood, the lymph and chyle, the saliva, and sometimes in the urine. In all these situations it is in much smaller proportion than the calcareous phosphate with which it is associated. In the bones, however, it is next in importance to the lime phosphate, being on the average one-seventh as abundant as that salt, and much more so than any of the remaining mineral ingredients. In the animal fluids, its solubility is accounted for by the presence of the alkaline chlorides or by that of free carbonic acid.

4. Magnesium Phosphate, $2(PO_4)Mg_3$.

Magnesium phosphate was formerly associated with the corresponding lime salt, under the name of the *earthy phosphates*, owing to certain resemblances in their chemical relations. Like the lime phosphate, which it everywhere accompanies, though for the most part in smaller quantity, it is present in all the tissues and fluids of the body. Thus in the bones the lime phosphate is in the proportion of 576 parts per thousand, while the magnesium phosphate forms only 12.5 parts. In the blood, the calcareous salt amounts to 0.30 part per thousand, the magnesium salt to 0.22 part; and in the milk there are 2.72 parts of lime phosphate to 0.53 part of magnesium phosphate. On the other hand, the salts of magnesium have been found in larger quantity than those of lime in the muscles, and nearly twice as abundant in the substance of the brain.

The magnesium phosphate is discharged, by the urine, in the average daily quantity of 0.6 gramme. The amount of both the earthy phosphates together is accordingly about 1 gramme per day; the magnesian salt being rather the more abundant of the two.

Both the magnesium phosphate and carbonate, of which latter salt traces occur in the blood, appear to have similar physiological relations with the corresponding salts of lime, and present the same features in their union with the tissues and their solubility in the animal fluids.

5. Sodium Chloride, NaCl.

This is undoubtedly the most important of the mineral constituents of the body, as regards its general distribution and its active part in the phenomena of nutrition. It is the most abundant of all, next to lime phosphate, and is present in all the animal tissues and fluids. Its entire quantity in the human body is estimated by Dr. Lankester at 110 grammes, or nearly one-quarter of a pound avoirdupois. In the blood it is nearly as abundant as all the other mineral ingredients together. Its proportion in various parts of the body is as follows:

Quantity of Sodium Chloride in 1000 Parts in the

Bones	7.02	Saliva	1.53
Blood	3.36	Milk	0.30
Bile	3.18	Lymph	5.00
Gastric juice	1.70	Sebaceous matter	5.00
Perspiration	2.23	Urine	5.50

One of the most important characters of this salt is its property of regulating the phenomena of endosmosis and exosmosis, or the transudation of fluids through the organic membranes. This property is shared by the other mineral ingredients of the blood, but is more important in the case of sodium chloride, owing to its preponderance in quantity over the rest.

As sodium chloride is present in all parts of the body, it is also an important ingredient of the food. It occurs in all animal food as a natural ingredient of the corresponding tissues. In muscular flesh, however, it is less abundant than potassium chloride, while, on the other hand, it is more abundant in the blood. It exists also in various kinds of vegetable food.

According to Boussingault, it is found in the following proportions in certain vegetable substances:

Proportion of Sodium Chloride in 1000 Parts in

Potatoes	0.43	Oats	0.11
Beets	0.66	Peas	0.09
Turnips	0.28	Beans	0.06
Cabbage	0.40	Meadow hay	3.28

The relative quantity of sodium chloride consumed in animal and vegetable food has not been determined. In regard to the demand for this salt, however, there is a striking difference between the carnivorous and herbivorous animals. The carnivora receive a sufficient supply with their natural food, and usually show a repugnance to salt as well as to salted meats. On the other hand, the horse and ruminating animals have an instinctive desire for salt. They greedily devour it, when offered to them, in addition to that naturally contained in their food, and it is shown by common experience that a liberal supply of salt is important for their healthy nutrition.

The same fact has been demonstrated in a more exact manner by the experiments of Boussingault.* This observer made a series of comparative investigations upon the growth of two sets of bullocks of the same age and vigor, and supplied equally with an abundance of ordinary nutritious food, those of one set receiving in addition each 34 grammes of salt per day. At the end of six months the difference in the aspect of the animals of the two sets began to be evident, and became more marked as time went on. The experiment lasted for a year, and at the end of that time both sets of animals had equally increased in weight; but those fed with ordinary food presented a

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* Chimie Agricole. Paris, 1854, p. 251.

rough and tangled hide, and a dull, inexcitable disposition, while in those which had received the additional ration of salt the hide was smooth and glistening, and the general appearance was vigorous and animated. While these animals, therefore, may subsist for a time upon the salt naturally contained in their food, an additional quantity is required to maintain the system in good condition for an indefinite period.

There is a similar necessity for salt as an addition to the food of the human species. No other condiment is so universally employed; and its use seems to be based upon an instinctive demand of the system for a substance which is necessary for the full performance of its functions. Beside other properties, it no doubt acts in a favorable manner by exciting the digestive secretions, and by assisting in this way the solution of the food. Food which is tasteless, however nutritious in other respects, is taken with reluctance and digested with difficulty; while the attractive flavor developed by cooking, and by the addition of salt and other condiments, excites the secretion of the saliva and gastric juice, and thus facilitates digestion. The sodium chloride taken with the food is afterward absorbed from the intestine, and deposited in various quantities in different parts of the body.

Notwithstanding various surmises which have been presented as to its possible decomposition and the recombination of its elements in the body, we have no certain knowledge of such changes taking place in the sodium chloride while a constituent part of the animal frame. It passes from the alimentary canal to the blood, from the blood to the tissues, and is finally discharged with the urine, mucus, and cutaneous perspiration in solution in these fluids. Under ordinary circumstances, much the largest proportion passes out by the kidneys. The entire quantity of sodium chloride discharged with the excretions by an adult man is about 15 grammes per day;* of which 13 grammes are contained in the urine, and 2 grammes in the perspiration. Thus, of all the sodium chloride contained in the body, considerably more than ten per cent. passes through the system in twenty-four hours. This plainly indicates its activity and importance in the internal changes of nutrition.

6. Potassium Chloride, KCl.

This substance is found in many, if not all, of the animal tissues and fluids, accompanying the sodium chloride, with which it is closely related in its physiological characters. It is especially abundant, as compared with sodium chloride, in the muscles and in the milk, less so in the blood, the gastric juice, the urine, and the perspiration. Both salts are neutral in reaction, and are retained in the liquid form in the blood and secretions by solution in the water of these fluids. Potassium chloride is introduced as an ingredient of both animal and

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* Neubauer und Vogel: Analyse des Harns. Wiesbaden, 1872, p. 54. Beneke: Pathologie des Stoffwechsels. Berlin, 1874, p. 322.

vegetable food, and is discharged with the mucus, the urine, and the perspiration.

7. Sodium and Potassium Phosphates, Na_2HPO_4 and K_2HPO_4.

These substances, associated under the name of the *alkaline phosphates*, are of great importance as ingredients of the animal body. They exist in all its solids and fluids, and in the latter are present in the liquid form by means of their ready solubility in water. They are no doubt useful in a variety of ways, but one of their most important characters is their alkaline reaction. This reaction is essential to a large number of the vital processes, and is present in all the animal fluids contained in the circulatory system, or in the closed cavities of the body. An acid reaction, on the other hand, belongs to but few of the animal fluids. One of these is a secretion employed in the digestive process; the rest are all discharged externally.

The following list shows the comparative frequency of alkaline and acid fluids in the human body:

FLUIDS WITH AN ALKALINE REACTION.

1. Blood-plasma.
2. Lymph.
3. Aqueous humor.
4. Cephalo-rachidian fluid.
5. Pericardial fluid.
6. Synovia.
7. Fluids of the living muscular tissue.
8. Mucus in general.
9. Milk.
10. Spermatic fluid.
11. Tears.
12. Saliva.
13. Bile.
14. Pancreatic juice.
15. Intestinal juice.

FLUIDS WITH AN ACID REACTION.

1. Gastric juice.
2. Perspiration.
3. Mucus of the vagina.
4. Urine.

If we take into account the carbonic acid exhaled with the breath, it is evident that an alkaline condition is in general characteristic of the internal fluids, while the products of excretion present an acid reaction.

Of the internal fluids the most essential is the plasma of the blood, since it supplies the materials of nutrition to the entire system; and its reaction has been found invariably alkaline, not only in man, but also in every species of animal in which it has been examined. This reaction is necessary to life, since Bernard demonstrated that an injection of dilute acetic or lactic acid into the veins of a living animal produces death even before the point of neutralization has been reached.

The alkaline reaction of the blood-plasma gives to this fluid its capacity for dissolving carbonic acid. According to Liebig, water which holds in solution one per cent. of sodium phosphate can absorb twice its usual proportion of carbonic acid; and the other alkaline salts have a similar dissolving action upon this gas. The blood as it circulates among the tissues absorbs from them the carbonic acid formed in their substance, and carries it away to be eliminated by the lungs. If this important property, which depends upon the alkalescence of the blood, be lost by its neutralization, the elimination of carbonic acid by the lungs is no longer possible, and the tissues become overloaded by its accumulation. This is probably the cause of death in Bernard's experiment.

The alkalescence of the blood-plasma is due in great measure to the alkaline phosphates, which are present in human blood in the proportion of 0.67 per thousand parts. A peculiar relation exists in this respect, for different classes of animals, between the alkaline phosphates and the alkaline carbonates, which are to be mentioned hereafter. Both these groups of salts have, in solution, an alkaline reaction; and both contribute to the alkalescence of the blood in man and animals. But in the carnivorous animals it is the phosphates which preponderate, while in the herbivora the carbonates are more abundant. In species fed upon both animal and vegetable food the two kinds of salts are present in nearly equal proportion; and in the same animal either the phosphates or the carbonates may be made to predominate by increasing the proportion of animal or vegetable food respectively. This is due to the fact that muscular flesh is comparatively abundant in phosphates, while vegetable matters abound in salts of the organic acids, which give rise by their decomposition in the system to carbonates of the same bases.

The alkaline phosphates are mainly derived from the food. They circulate with the animal fluids, and are finally excreted under their own form in the perspiration, the mucus, and the urine. A partial exception to this rule is found in the urine, where a portion of the alkaline sodium phosphate is replaced by the acid biphosphate, giving to the whole fluid an acid reaction. The explanation of this change, as generally understood, is the following. A nitrogenous organic acid of new formation, namely, uric acid, makes its appearance in the system, and is excreted by the urine, in the form of a neutral combination, as sodium urate. It is believed to combine, at the time of its formation, with a portion of the sodium of the sodium phosphate, and the remainder of this salt is thus converted into a biphosphate. The normal reaction of the urine is therefore really due to the formation in the body of an acid substance; although the substance so produced does not appear in the urine as the immediate cause of its acidity.

There is also evidence that a certain amount of phosphoric acid is formed in the body by the process of oxidation. A substance containing phosphorus in organic combination, known as "lecithine," exists in various parts of the system, especially in the blood, brain, and nerves, and is also taken with certain kinds of food; but no such substance is met with in the excreted fluids, where phosphorus exists only in the form of the phosphatic salts. It is no doubt oxidized in the internal transformation of the organic substances, thus becoming phosphoric acid, which in turn unites with the alkaline bases to form phosphates. In this way some of the superabundant acid is produced, which gives rise to the reaction of the excreted fluids.

The sodium and potassium phosphates, including the acid biphosphate, are discharged with the urine to the amount of about 4.5 grammes per day.

8. Sodium and Potassium Carbonates, CO_3Na_2 and CO_3K_2.

The alkaline carbonates, as mentioned above, are associated with the phosphates in all the more important fluids of the body. They are readily soluble in watery fluids, and assist in producing the alkalescence of the blood and secretions. They are partly introduced with the food, where they exist in limited quantity, but they are formed in great measure within the body by the decomposition of other salts of vegetable origin. Certain fruits and vegetables, such as apples, cherries, grapes, potatoes, carrots, and the like, contain malates, tartrates, and citrates of the alkaline bases. It has been often observed that after the use of fruits and vegetables containing the above salts, the urine becomes alkaline from the presence of the carbonates. Lehmann found, by experiments upon his own person, that within thirteen minutes after taking 15.5 grammes of sodium lactate, the urine had an alkaline reaction. He also observed that a solution of this substance injected into the jugular vein of a dog, caused the urine to become alkaline at the end of from five to twelve minutes. The conversion of these salts into carbonates takes place, therefore, not in the intestine, but in the blood. The same observer found that, in many persons living on a mixed diet, the urine became alkaline in two or three hours after swallowing 0.65 gramme of sodium acetate.

The organic acid in these cases is decomposed; and the original salts are thus replaced by the alkaline carbonates, which appear in the urine and modify its reaction as above described.

A preponderance of vegetable food, accordingly, influences the quantity of the alkaline carbonates in the system, and consequently the reaction of the excretions. As a rule, the urine of man and of the carnivorous animals is clear and acid, while that of the herbivora is alkaline and turbid with calcareous deposits. Such turbid and alkaline urine will often effervesce with acids, showing the presence of carbonates in considerable quantity. This difference depends upon the alimentation of the animal, and although in carnivorous and herbivorous animals under ordinary conditions the urine is respectively acid and alkaline, if they be both deprived of food for a few days the urine becomes acid in both, since they are then, in each instance, living upon their own tissues. Furthermore, a rabbit, whose urine is turbid and alkaline while feeding on fresh vegetables, if kept on a diet of animal food, soon produces an excretion which is clear and acid. The reverse effect is produced upon a dog by changing his food from meat to vegetable matters. Finally, the urine of the young calf while living on the milk of the mother is clear and acid; but after the animal has been weaned and feeds upon vegetable matter, its urine becomes alkaline and turbid, like that of the adult animal.

9. Sodium and Potassium Sulphates, SO_4Na_2 and SO_4K_2.

The sulphates are constant ingredients of the body, and are found in several of the animal fluids, including the blood, the lymph, the aqueous humor, milk, saliva, mucus, the perspiration, and the urine. They are usually, however, in small quantity, as compared with other saline matters. In the blood and the lymph they are much less abundant than either the chlorides, phosphates, or carbonates. In the milk and the saliva there is hardly more than a trace of them; and they have not been found in the bones, the gastric juice, the bile, or the pancreatic juice. They are most abundant in the urine, where they amount to rather more than one-half the quantity of the phosphates, and they are found also, in small proportion, in the feces.

The sulphates are introduced into the body, to some extent, with the food and drink. They are present, in minute quantity, in muscular flesh and in the yolk of egg. They exist also in certain vegetable products, such as the cereal grains, fruits, and tuberous roots, where they are less abundant than the phosphates, though often more so than the chlorides. Spring and river water, used for drink, usually contains sulphates, including sulphate of lime, varying in amount, according to Payen, from .003 to .06 per thousand parts. In the water of the Croton river, with which the city of New York is supplied, they amount, as shown by Prof. Chandler, to a little more than .007 per thousand parts.

Beside the sulphates introduced with the food and drink, a certain amount of sulphuric acid originates within the body by oxidation, in a mode analogous to that already described for phosphoric acid. The albuminous substances, which form so important a part of the solid food, contain sulphur as one of their constituent elements, and a considerable quantity is accordingly introduced into the system in the form of organic combination. The entire quantity of sulphur, thus forming part of the organic matters of the human body, amounts, according to Payen,* to about 110 grammes; and at least 1 gramme is taken daily with the albuminous ingredients of the food. A portion is expelled with the daily exfoliation of the hair, nails, and epidermis; but no such sulphurous organic compound is discharged by the urine and feces except in insignificant quantity. On the other hand, the sulphates are comparatively abundant in the excretions. While they are to be found in the blood only in the proportion of 0.28 per thousand, they exist in the urine in the proportion of from 3.00 to 7.00 parts per thousand, and are discharged by this channel to the amount of about 4 grammes per day.

These facts indicate that a notable quantity of sulphuric acid is formed

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* Substances Alimentaires. Paris, 1865, p. 68.

in the body, during the decomposition of albuminous matters, by oxidation of their sulphur. This is confirmed by the fact that the quantity of sulphuric acid in the sulphates eliminated by the kidneys is increased by a flesh diet, and also by the administration of sulphur or a sulphuret.* Dr. Parkes estimates the quantity of sulphuric acid thus produced in the system as about double that taken in the form of sulphates with the food and drink. It unites with the alkaline bases, displacing the weaker acids with which they were combined, and thus contributes indirectly to the general acid reaction of the excreted fluids.

The foregoing substances are the most important of the inorganic ingredients of the body. They are distinguished from the organic ingredients by their comparatively simple chemical composition, by their external origin, and by the part which they take in the constitution and nourishment of the animal frame. They are derived for the most part from without, being taken directly from the materials of the inorganic world. There are some exceptions to this rule; as in the case of the alkaline carbonates formed in the body by decomposition of the salts of the vegetable acids; of the sodium biphosphate produced from the neutral phosphate by the action of an organic acid, and of the phosphates and sulphates formed by the process of oxidation. But the greater part of the substances belonging to this class are introduced with the food, and absorbed by the animal tissues and fluids, in the form under which they exist in external nature. The lime carbonate of the bones, and the sodium chloride of the blood and the tissues, are the same substances as those met with in calcareous rocks, or in sea water.

In the process of internal nutrition they are exempt, as a general rule, from chemical change. Some of them, such as the lime and magnesium phosphates, are mostly deposited in the solid parts, and are renewed but slowly, contributing mainly to the physical properties of the tissues, and taking a comparatively small share in the actions of repair and waste. Others, such as water and the alkaline chlorides, are introduced and discharged in abundance, passing rapidly through the system, and playing an important part in the phenomena of solution and transudation. Others, such as the alkaline phosphates and sulphates, when formed in the body by oxidation, appear in the urine as a residue from the decomposition of other substances.

The larger proportion, however, of the inorganic matters are reabsorbed from the tissues in which they were deposited, and discharged unchanged with the excretions. They do not, for the most part, participate directly in the chemical phenomena of the living body; but rather serve to facilitate, by their presence, the necessary changes of nutrition in other ingredients of the animal frame.

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* Neubauer und Vogel: Analyse des Harns. Wiesbaden, 1872, pp. 356, 357.

CHAPTER III.

HYDROCARBONACEOUS SUBSTANCES.

THE members of this class are distinguished from the preceding by their organic origin. They appear as products of the nutritive actions of organized beings, and are not introduced ready formed from the inorganic world. They exist both in vegetables and in animals. In the former they are produced as new combinations, under the influence of the vegetative process; and even in animals, which feed upon vegetables or upon other animals, they are so modified by digestion and assimilation that they present themselves, as final constituents of the body, under new and specific forms. They all consist of carbon, hydrogen, and oxygen, of which carbon is present by weight in especially large proportion, forming from 44 to 84 per cent. of the entire substance. Owing to the absence of nitrogen, which is an important element in organic matters of the following class, they are known as "non-nitrogenous" substances. They are divided into two principal groups, namely: the *carbo-hydrates*, or substances containing carbon, with hydrogen and oxygen in the proportions to form water; and the *fatty matters*, in which the proportions of carbon and hydrogen are increased, while that of oxygen is diminished. The group of the carbo-hydrates includes starch, glycogen, and sugar.

Starch, $C_6H_{10}O_5$.

A special physiological interest attaches to starch from the fact that it is the first organic substance produced, in vegetation, from inorganic materials. The animal body is incapable of forming organic matter, and must be supplied with these substances in the food. But vegetables have the power of combining inorganic elements in such a way as to produce a new class of bodies, peculiar to the organic world, and capable of serving for nutrition. This is shown by numerous experiments, in which seeds or young plants, artificially cultivated in a soil of clean sand, moistened only with solutions of mineral salts, have germinated, grown, and fructified, increasing, many times over, the quantity of organic material which they contained at the beginning.

This production of organic matter takes place in the leaves and other green tissues of growing plants, under the influence of the solar light; and the first substance which makes its appearance under these conditions is nearly always starch. It is produced from two inorganic matters absorbed from without, namely, carbonic acid and water, which are deoxidized by the vegetable tissues, and their elements combined to form a carbo-hydrate. This is proved by the fact that oxygen is exhaled, during the vegetative process, in the same, or nearly the same, proportion as that in which it originally existed in the carbonic acid; and the new substance produced contains hydrogen and oxygen in the proportions to form water. The production of starch in growing vegetables is therefore represented by the following formula:

$$\underset{\text{Carbonic Acid.}}{6\,CO_2} + \underset{\text{Water.}}{5\,H_2O} - O_{12} = \underset{\text{Starch.}}{C_6H_{10}O_5}.$$

The production of starch in this way by vegetation is a phenomenon of the first importance in the economy of living beings. It is the only natural process known to take place on the earth by which oxygen is set free from its actual combinations. It is a reduction of two compounds in which the oxygen affinity of carbon and hydrogen was fully satisfied, resulting in the formation of an organic matter capable of reoxidation. The new substance so produced has therefore a power of combination, which may be afterward brought into activity under requisite conditions, and which is the theoretical basis of all force manifested by the living organism.

There are two conditions requisite for the formation of organic matter by vegetable tissues: First, the access of solar light, either by direct sunshine or by diffused daylight, and, secondly, the existence in the living plant of the green coloring matter known as "chlorophylle." Green vegetables, which absorb carbonic acid and exhale oxygen in the sunshine, cease to do so when daylight disappears, and remain inactive in this respect during the night. On the other hand, colorless vegetables, and the uncolored portions of green plants, have no reducing action, even in the daytime.

The materials for this reduction process in vegetables, namely, carbonic acid and water, are supplied from the atmosphere and the soil. As the atmosphere contains about .05 per cent. of its volume of carbonic acid, and as the column of air above each square metre of surface, at the ordinary barometric pressure, weighs a little over 10,000 kilogrammes, this would give, by weight, 7.5 kilogrammes of carbonic acid to the square metre, equivalent to 30,390 kilogrammes, or rather more than thirty tons, over each acre of land. From this abundant reserve, the carbonic acid is supplied for vegetation. It is absorbed directly by the foliage in contact with the atmosphere, and, brought down in solution by the rain, it is taken up by the roots and transferred to the leaves by the vegetable juices. The activity of the reducing process has been measured by Boussingault.* He found that a single fresh oleander leaf in sunshine decomposed in two successive days nearly 49 cubic centimetres of carbonic acid; and, as a mean of six similar experiments, each square centimetre of leaf surface decomposed 1.33 cubic centimetres of the gas, exhaling an equal volume of free oxygen. It is estimated by Hoppe-Seyler, that, considering the amount of oxygen consumed by animal organisms and the time during which these organ-

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* Comptes rendus de l'Académie des Sciences, Paris. Tome LXI., pp. 498, 502.

isms have existed upon the earth, the whole of the free oxygen now present in the atmosphere must have once been liberated from its combinations by the vegetative process.

When first produced in the vegetable tissue, starch is in the form of minute, rounded, homogeneous granules. These granules afterward increase in bulk, reaching a size which varies in different instances from 2.5 to 50 or 60 mmm* in diameter. They often acquire a definite structure, each granule exhibiting under the microscope a series of layers or concentric markings, arranged round a single point, like the scar of a ripe seed, which is termed the "hilum." These characters differ more or less, according to the period of growth of the starch granule and the tissue from which it is derived; but they are sufficiently well marked in nearly all the varieties which are prepared for food or employed in the arts. The starch grains of the potato are among the most characteristic.

FIG. 2.

GRAINS OF POTATO STARCH.

The successive layers of which starch granules are composed differ mainly in their consistency, being alternately harder and softer, thus producing a corresponding difference in refractive power, and an appearance of concentric striation. Each granule, furthermore, consists of two substances, intimately mingled in every part of its mass, which resemble each other completely in chemical composition, but differ in solubility. These substances are, first, *granulose*, which may be extracted from the starch grain by boiling water; and, second, *cellulose*, which remains undissolved. The granulose is usually much the more abundant of the two, but the cellulose has so marked a consistency that it retains the form and laminated appearance of the starch grain, after extraction of the granulose, though reduced to five or six per cent. of its original weight.

As starch is the earliest and simplest product of vegetation, it is most abundantly diffused through the vegetable kingdom, and exists, for at least a certain period, in every plant which has yet been examined for it. It occurs especially in seeds, in the cotyledons of the young plant, in roots, tubers, and bulbs, in the pith of stems, and sometimes in the bark. It is very abundant in corn, wheat, rye, oats, and rice, in the

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* The sign mmm. stands for *micro-millimetre*; that is, the one-thousandth part of a millimetre. A millimetre is very nearly equivalent to one twenty-fifth of an inch; and a micro-millimetre, accordingly, is about $\frac{1}{25000}$ of an inch.

potato, in peas and beans, and in most vegetable substances used as food. It constitutes almost entirely the preparations known as sago, tapioca, arrow-root, and maizena, which are nothing more than varieties of starch, extracted from different plants.

The following list, compiled mainly from the tables of Payen,* shows the percentage of starch in various kinds of food:

QUANTITY OF STARCH IN 100 PARTS IN

Wheat	57.88	Potatoes	20.00
Rye	64.65	Sweet potatoes	16.05
Oats	60.59	Peas	37.30
Barley	66.43	Beans	33.00
Indian corn	67.55	Flaxseed	23.40
Rice	88.65	Chocolate nut	11.00

Starch derived from all these sources has essentially the same chemical composition, and may be recognized by the same tests. It is insoluble in cold water, but if treated with about twenty times its weight of boiling water its granules swell, become gelatinous and amorphous, combine with a certain proportion of water, and fuse into an opaline liquid, which is thicker or thinner according to the quantity of water present, and which solidifies, on cooling, into a nearly homogeneous paste, the water remaining united with the amylaceous matter. The starch is then in a pasty and amorphous condition, its chemical properties remaining essentially unaltered. If treated with 100 or 150 parts of water at the boiling temperature it makes a liquid which does not gelatinize on cooling; but the imperfectly liquefied portions, containing the insoluble cellulose, gradually subside as a turbid deposit, while the soluble starch remains above, forming a clear and colorless liquid.

Starch is especially distinguished by its property of striking a blue color with iodine. This reaction will take place even with raw starch, and its granules may be recognized under the microscope by this means. It is still more prompt when the starch has been boiled to a paste, and especially when it is in solution. A minute quantity of tincture of iodine, added to a starch solution, produces at once a deep blue color, which may be largely diluted without losing its characteristic tinge. This test, however, must be employed at a moderate temperature. If the solution be too hot, no visible reaction will occur; and even after it has taken place, if heat be applied the blue color will disappear, to return again after cooling down to the proper temperature. The iodine must also be used in a free state. If added in the form of a soluble iodide it will produce no effect, since the starch has not sufficient affinity to withdraw it from its union with other matters. Finally, no third substance must be present which would be capable of combining with the iodine and thus preventing its action on starch. Many animal fluids, such as the serum of blood, saliva, mucus, and urine,

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* Substances Alimentaires. Paris, 1865.

contain ingredients which interfere with the reaction, and may even dissipate the blue color after it has been produced. These substances must be removed before the application of the test, or the iodine must be added in excess to allow for action on the starch. With these precautions it forms a valuable test.

Starch has the property of being changed, under certain conditions, into two other substances.

1. If subjected to torrefaction, that is, a dry heat of 210° C. (about 400° F.), it is converted into *Dextrine*, a gummy substance soluble in water, so called from the fact that in solution it rotates the plane of the polarized ray toward the right.* Dextrine has the same chemical composition with starch, but its physical properties are different, and when treated with iodine it takes a rosy red instead of a blue color. The same transformation of starch is accomplished by boiling with a dilute acid; the solution becoming in a few minutes clear and liquid, and changing its reaction with iodine. Finally, in the germination of certain starchy seeds, such as the cereal grains, the transformation of starch into soluble dextrine takes place in the presence of moisture at moderate temperatures, under the influence of a nitrogenous ferment.

2. Starch may be converted into *Sugar*. When a starch solution or thin starch paste is boiled with a dilute acid, it is first changed, as described above, into dextrine. But by continued boiling for several hours it begins to be further transformed into sugar, and at last it passes wholly into the saccharine condition. The same conversion takes place during the germination and growth of plants, where sugar makes its appearance at the expense of the starch, as soon as the requisite moisture and warmth are supplied. This is the usual source of sugar in vegetable juices, the starch previously stored up being changed into sugar by the molecular actions going on in the vegetable fabric. Finally, various nitrogenous animal substances, like those in the saliva or the intestinal juices, at the temperature of 38° C., have the same effect. This is the change which normally takes place during digestion. Starchy substances, when taken as food, are changed into sugar in

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*A ray of light which has passed through certain crystalline bodies, such as a "Nicol's prism" of Iceland spar, is found to be *polarized;* that is, it has acquired opposite and complementary properties in two different directions. For if received by a second similar prism, which is equally transparent in all positions to ordinary light, the polarized ray will pass through it only when the principal section of the second prism is parallel with that of the first; but when the second prism is turned round 90°, the light is arrested. Now if certain organic substances in solution be placed between the two prisms, it is found that they have the effect of changing the angle at which the second prism must stand in order to arrest or transmit the light from the first. In other words, the plane of polarization of the polarized ray has been deviated or rotated by the organic liquid. Some substances deviate the plane of polarization toward the right, others toward the left. The specific rotary power of each is estimated for a solution of standard strength and quantity, for yellow light, and is indicated in degrees of the circle. The specific rotary power of dextrine is 118°.

the alimentary canal, and under that form are absorbed into the circulation.

It is evident, therefore, that starch, although the earliest organic matter produced by vegetation, is not the form under which it takes part in nutrition. It is mainly formed in the leaves, but remains there only as a temporary product. Its granules become liquefied, and it is transported, as soluble dextrine or sugar, to other and distant parts of the plant. There it resumes the solid form, and is either changed into cellulose, for the woody fibre of the growing tissues, or is deposited as starch in the seeds, tubers, or fleshy roots of the plant. It is in these situations that the principal accumulation of starchy matter takes place; and it there forms a reserve material, to be afterward employed for the nutrition of animals, or for the growth of the young plant. In either case it again undergoes a preliminary transformation. In the germination of a seed, its starch is liquefied by conversion into dextrine and sugar, before it can be appropriated by the growing tissues; and if consumed as food by man or animals, it undergoes the same transformation in the digestive process.

Sugar.

The proximate principles designated under this name include a variety of substances which have certain well-marked characters, and are of frequent occurrence in both animal and vegetable juices. They are crystallizable and soluble in water, and have, when in solution, a sweet taste, which, in some varieties, is very highly developed. They are all decomposed by heating with sulphuric acid; their hydrogen and oxygen being driven off, while the carbon remains behind as a black deposit. In this condition they are said to be carbonized. The proportions in which they occur in various articles of food, according to the tables of Payen, Von Bibra, and a few other observers, are as follows:

QUANTITY OF SUGAR IN 100 PARTS IN

Cherries	18.12	Wheat flour	2.33
Apricots	16.48	Rye flour	3.46
Peaches	11.61	Barley meal	3.04
Pears	11.52	Oat meal	2.19
Juices of sugar-cane	18.00	Indian corn meal	3.71
Sweet potatoes	10.20	Cow's milk	5.20
Beet roots	8.00	Goat's milk	5.80
Parsnips	4.50	Beef's liver	1.79

The most important varieties of this substance, in a physiological point of view, are glucose, cane sugar, and milk sugar.

1. Glucose, $C_6H_{12}O_6$.

Glucose, also called *grape sugar*, from its abundance in the juice of the ripe grape, may be considered as the representative of the saccharine substances. It occurs more frequently than any other in the animal fluids, being found in the juices of the liver, in the chyle, the blood, and the lymph. In diabetes it is abundantly excreted with the urine.

It is also found in the juices of many plants, in various sweet fruits, and in honey, where it is associated with certain other varieties. It is freely soluble in water. Its solution has a moderately sweet taste, and deviates the plane of polarization toward the right 53.5°.

It is this form of sugar which is produced from starch by boiling with dilute acids, by the action of the digestive fluids, and in the plant during germination. The change consists in the assumption by starch of the elements of water, the new substance thus produced being still a carbo-hydrate. The transformation of starch into glucose is therefore represented as follows:

$$\underset{\text{Starch.}}{C_6H_{10}O_5} + \underset{\text{Water.}}{H_2O} = \underset{\text{Glucose.}}{C_6H_{12}O_6}.$$

Glucose may be recognized in solution by various tests. First, the *action of alkalies at a boiling temperature.* If a solution of glucose be heated with a solution of potassium hydrate, the sugar is decomposed and the liquid assumes, first, a yellowish and then a brown color, which becomes deeper in proportion to the amount of glucose and alkali in the solution. This is not an exclusive test for glucose, as some other organic matters are discolored in a similar way by the strong alkalies; but it will serve to distinguish it from cane sugar, which does not possess this property.

Secondly, the test most commonly employed for glucose depends upon its power of *reducing the salts of copper in a boiling alkaline solution.* This test, which is known as "Trommer's test," is applied in the following manner: A small quantity of copper sulphate in solution is added to the suspected liquid and the mixture rendered alkaline by the addition of potassium hydrate. The solution then takes a blue color. On boiling the mixture, if glucose be present, the copper suboxide is thrown down as an opaque red, yellow, or orange-colored deposit; otherwise no change takes place. In this reaction the sugar, which is oxidized at a high temperature under the influence of the alkali, takes a portion of its oxygen from the copper salt and reduces it to the form of insoluble suboxide.

Some precautions are necessary in the use of this test. As a general rule, the quantity of copper sulphate added to the liquid under examination, should be only sufficient to give a distinct blue tinge after the addition of the alkali. If the copper salt be used in excess, the sugar in solution may not be sufficient to reduce the whole of it; and that which remains as a blue sulphate may mask the yellow color of the suboxide thrown down as a deposit. This difficulty may be removed by due care in the proportion of the ingredients.

Furthermore, there are some albuminous substances which interfere with the test, and prevent the reduction of the copper, even when sugar is present. Certain animal matters, to be described hereafter, which are liable to occur in the gastric juice and in the blood, have this effect.

The ordinary ingredients of the urine also interfere with Trommer's test, so that no precipitate takes place when glucose is present, although the liquid turns yellow on boiling. A very large proportion of glucose may be added to fresh urine without giving rise to a pulverulent precipitate on the application of the test; notwithstanding that, if dissolved in pure water, it will react when present in the proportion of one part to 10,000. The interference of urine with Trommer's test depends, not upon its preventing deoxidation, but upon its retaining the reduced copper oxide in solution, since the color of the mixture changes from blue to yellow, although no precipitate takes place. It is also shown by Dr. Fowler* that if the precipitate resulting from Trommer's test with a watery solution of glucose be added to boiling urine, it is redissolved. The same observer has devised a method of applying the test to urine containing glucose. A certain quantity of urine can dissolve only a certain amount of copper oxide; and if the copper sulphate solution be added to a specimen of saccharine urine in large proportion, the excess will be precipitated and show itself as a deposit. A copper sulphate solution, made in the proportion of 1 part copper sulphate to 7.5 parts of water, and added to saccharine urine to the amount of one-half or one-third its bulk, will generally produce a satisfactory reaction.

All such sources of error may be avoided by treating the suspected fluid with animal charcoal, or by evaporating it to dryness, extracting the dry residue with alcohol, and then dissolving the dried alcoholic extract in water, before applying the test. Either of these processes will remove the substances liable to interfere with the test.

A more delicate reagent for glucose is that known as "Fehling's liquor," which is an alkaline solution of a double copper and potassium tartrate. It is made as follows:

Pure crystallized copper sulphate	40	grammes.
Neutral potassium tartrate	160	"
A solution of sodium hydrate of the specific gravity 1.12	650	"

The neutral potassium tartrate, dissolved in a little water, is first mixed with the solution of sodium hydrate. Then the copper sulphate, dissolved in 160 cubic centimetres of water, is gradually added to the alkaline liquor, which assumes a clear, deep blue color. The whole is finally diluted with water to the volume of 1154.4 cubic centimetres. If one drop of this liquid be added to one cubic centimetre of a saccharine solution and heat applied, it will detect one-fifteenth of a milligramme of glucose by the reduction of the copper oxide. One advantage of this test is that the quantity of copper salt contained in a given volume is accurately known, and consequently the amount of glucose in any solution may be determined by the quantity of test liquid which it decomposes at a boiling temperature. One cubic centimetre of Fehling's liquor is exactly decolorized by $\frac{1}{200}$th of a gramme of glucose.

An inconvenience connected with Fehling's liquor is that, by expo-

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* New York Medical Journal, June, 1874, p. 632.

sure to air and light, it undergoes an alteration, in which some of its tartaric acid is replaced by carbonic acid. In this condition it will partially precipitate on boiling, even without the presence of sugar. It should, therefore, be kept in bottles which are quite full and protected from the light; and, whenever a suspected fluid is to be examined, a small portion of the test-liquor should be previously boiled, to make sure that it has not undergone decomposition. Although by exposure, at a summer temperature, Fehling's liquor may become altered at the end of a week, yet if protected from the light, in carefully closed and full bottles, it can be kept unchanged for several years.

Thirdly, one of the most marked properties of glucose, available as a test, is its capacity for *fermentation.* If a small quantity of beer-yeast be added to a glucose solution, and the mixture kept at a temperature of 25° C., after a short time it becomes turbid. It then begins to liberate carbonic acid, which is partly dissolved in the liquid and is partly given off in the form of gas bubbles, which rise to its surface. From this circumstance the process has received the name of "fermentation" or boiling. At the same time the sugar is gradually destroyed and alcohol appears in its place. Finally the whole of the glucose is decomposed, having been converted principally into alcohol and carbonic acid. The transformation is expressed as follows:

$$\underset{\text{Glucose.}}{C_6H_{12}O_6} = \underset{\text{Alcohol.}}{2C_2H_6O} + \underset{\text{Carbonic Acid.}}{2CO_2}.$$

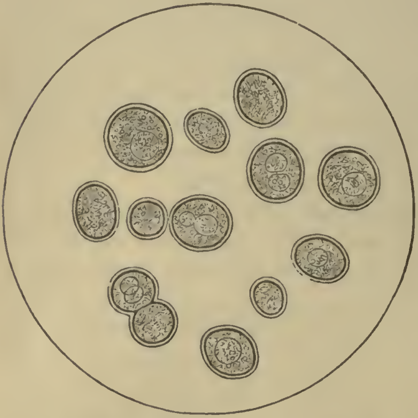
When this change is complete, the fermentation stops and the liquid becomes clear, its turbid contents subsiding to the bottom as a whitish layer. This layer is itself found to consist of yeast, which has increased in quantity over that originally added, and is capable of exciting fermentation in other saccharine liquids.

If, instead of pure glucose, we employ the expressed juices of certain fruits, like those of the grape, which contain albuminoid matters in addition to glucose, fermentation begins after a certain period of exposure, and goes on with the same phenomena as before. This is the source of all the vinous and alcoholic fluids used by man; namely, the fermentation of fluids containing glucose or a similar saccharine substance.

The fermentation of glucose is due to the action of a colorless microscopic fungus, known as *Saccharomyces.* This plant consists of cells, which multiply by a process of budding, but do not produce filaments, nor any compound vegetable fabric. The species present in beer-yeast is the "Saccharomyces cerevisiæ." Its cells are usually rounded in form, sometimes oval (Fig. 3). They vary in size, the greater number having a diameter of about 10 mmm. They have a thin investing integument, which incloses a finely granular semi-solid substance, often containing rounded cavities or vacuoles filled with fluid. The cells are mostly isolated, but occasionally two of them may be seen adhering together. There is a small amount of intercellular liquid, containing albuminous matter and mineral salts.

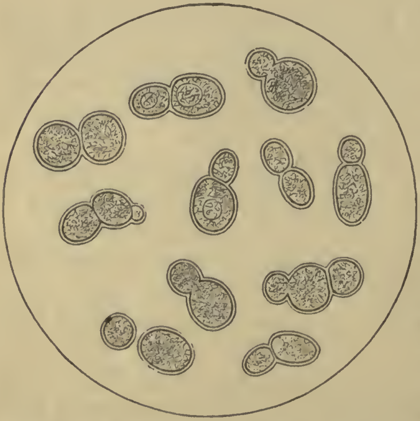
When yeast is added to a warm solution of glucose, the cells of the yeast-plant after a short time begin to multiply by budding. The buds increase rapidly in size, and, when the young cell has become nearly as large as its parent, it usually separates and begins an independent existence. While in this condition the cells are mostly oval in form, with an average diameter of but little more than 8 mmm. Often two or three are seen connected together, forming moniliform chains. It is by the active growth and development of the cells during this process that the glucose of the solution is decomposed, and alcohol and carbonic acid produced in its place. Another species of saccharomyces forms the fungus of bread-yeast, and a third the ferment of grape-juice, by which it is made to undergo the vinous fermentation.

Fig. 3.



Saccharomyces Cerevisiæ, in its quiescent condition; from deposit of beer-yeast, after fermentation.

Fig. 4.



Saccharomyces Cerevisiæ in active germination. From fermenting saccharine solution.

When fermentation is used as a test, a little beer-yeast is added to the supposed saccharine fluid, and the mixture kept at the temperature of 25° C. The gas given off during the process is collected and examined, and the remaining fluid is purified by distillation. If the gas evolved be carbonic acid, and if the distilled liquid contain alcohol, there can be no doubt that a fermentable sugar was present in the solution. Glucose undergoes fermentation more readily and more completely than the other varieties of sugar.

2. Lactose, $C_{12}H_{24}O_{12}$, *Sugar of Milk.*

Lactose is the saccharine ingredient of milk, the only fluid in which it is known to occur. It is less freely soluble than glucose, and is less sweet to the taste. In watery solution it rotates the plane of polarization to the right 58°.20. In chemical composition it is isomeric with glucose, which it resembles in being decomposed and turned brown by boiling alkalies, in reducing the copper-oxide in Trommer's and Fehling's tests, and in undergoing the alcoholic fermentation by the influence of yeast. It enters into fermentation, however, very slowly, as compared with glucose, and the process is usually incomplete. In the fermentation of milk, a part of its sugar is converted into lactic acid, $C_3H_6O_3$, also a carbo-hydrate. By boiling with dilute sulphuric or hydrochloric acid, lactose becomes readily and completely fermentable. This sugar forms an important element in the food of the infant, in which it is a constant ingredient. It is formed in the mammary gland, probably by transformation from glucose, but the exact method of its production is unknown. It is discharged with the milk, as a reserve material for the nutrition of the infant.

3. **Saccharose,** $C_{12}H_{22}O_{11}$, *Cane Sugar.*

This variety, the oldest known species of sugar, is derived from the juices of the sugar-cane, where it exists in great abundance. It solidifies, on cooling from a hot concentrated solution, in white granular crystalline masses; the form in which it is generally used for culinary purposes. If crystallized more slowly it furnishes large, colorless, prismatic crystals, known as "rock candy" or "sugar candy." This sugar is also obtained from the juices of the beet-root, and, imperfectly purified, from those of the sorghum and the sugar-maple. It exists to some extent in the green stems of Indian corn, in sweet potatoes, in parsnips, turnips, and carrots, and in the spring juices of the birch and walnut trees. Honey is a mixture of glucose and saccharose with various other substances.

Cane sugar originates from glucose, in the process of vegetation, by a change the reverse of that by which glucose is formed from starch, that is, by dehydration. A comparison of the chemical composition of the two substances will show the manner in which the transformation takes place, namely:

$$\underset{\text{Glucose.}}{2(C_6H_{12}O_6)} - \underset{\text{Water.}}{H_2O} = \underset{\text{Cane Sugar.}}{C_{12}H_{22}O_{11}}.$$

Saccharose is the most soluble of the sugars, and has the strongest sweet taste. It rotates the plane of polarization to the right 73°.84. It differs from glucose by the fact that it is not turned brown by boiling with an alkali, and does not reduce the copper-oxide in Trommer's test. It may be converted into glucose, however, by a few seconds' boiling with a dilute mineral acid, and will then react promptly with boiling alkalies and with Trommer's test. Cane sugar is not immediately fermentable, but by contact with yeast it is after a time changed into glucose, and finally enters into fermentation. In the living vegetable tissues it represents a reserve material, and is subsequently reconverted into glucose for the purposes of nutrition.* When taken as food, it is transformed into glucose by the intestinal fluids.

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*Mayer: Agrikultur-Chemie. Heidelberg, 1871. Band I., p. 122.

Sugar and starch, accordingly, in all their varieties, are closely allied, both in their chemical and physiological relations. They are all carbohydrates, and their mutual convertibility in the vegetative process has been shown by abundant investigations. Starch and sugar, in the living plant, represent the same nutritive material under two different conditions; starch having the form of a solid deposit, glucose that of solution and activity. The organic substance passes from one to the other of these two conditions by hydration or dehydration. It is at last either decomposed in the immediate changes of nutrition, or is stored up as a deposit for future consumption.

Glycogen, $C_6H_{10}O_5$.

Glycogen, so called from its capacity for the production of glucose, is an amylaceous substance of animal origin. It is isomeric with starch and dextrine, and resembles the latter in its physical properties, except that a watery solution of dextrine is clear, while that of glycogen is opalescent, and that when treated with iodine, dextrine in solution gives a rosy red, glycogen a deep brown-red color. It is insoluble in alcohol and in ether, but soluble in water, either cold or hot. Its watery solution deviates the plane of polarization strongly to the right, its specific power of rotation for yellow light being about 130°.

This substance is constantly present in the tissue of the liver in all vertebrate animals, in the healthy condition. It is found at an early period of development in the integument and mucous membranes of the embryo, in a portion of the placenta and amnion, in the muscles during their formative condition, and in the pulmonary tissue. It does not exist at this time in the liver, or in any other of the glandular organs. But about the middle of fœtal life it begins to be found in the liver, where it increases in quantity, at the same time gradually disappearing from the other organs; and after birth it is a characteristic and abundant ingredient of the liver alone. It has been found, however, in moderate and varying amount in the muscles of some adult quadrupeds and birds, and in considerable quantity in molluscous animals, as the oyster and the cockle-shell.

Glycogen is obtained from the liver of a well-fed animal in the following manner: The organ is taken out immediately after death and cut into small pieces, which are then coagulated by a short immersion in boiling water. This arrests the changes which would otherwise take place under the influence of a ferment contained in the hepatic juices. The coagulated tissue is then ground to a pulp and boiled for half an hour with a small quantity of water, making a concentrated decoction, which is afterward treated with animal charcoal, to remove the coloring matters, and filtered. The filtered decoction is opaline, but does not hold in suspension any solid granular matters visible with the microscope. It is allowed to fall by drops into strong alcohol, by which the dissolved glycogen is precipitated, subsiding to the bottom as a white deposit. It is still contaminated by a little glucose, a certain quantity of biliary salts, and some albuminous matters. The glucose and biliary salts are removed by washing the precipitate with alcohol. The remainder is then boiled for a quarter of an hour with a concentrated solution of potassium hydrate, which dissolves the albuminous matters, but does not affect glycogen. After filtration it is again dissolved in water, the traces of alkali removed by the addition of a little acetic acid, and the glycogen re-precipitated by alcohol in excess. It is then dried and may be kept in the form of a white pulverulent mass, which retains its properties for an indefinite time.

In watery solution it exhibits the characteristic properties of an amylaceous substance, being converted into sugar by all agencies which have a similar effect on starch, namely, by boiling with a dilute mineral acid, and, at a moderately warm temperature, by the contact of saliva, the pancreatic or intestinal juices, or the serum of blood. If allowed to remain in the liver after death, or brought in contact with its tissue after removal, a portion is transformed into glucose by the albuminous matters of the hepatic substance.

The quantity of glycogen in the liver varies, with the kind of food used, from about 7 to 17 per cent. It is more abundant with vegetable than with animal food, and is most abundant of all under a diet of carbohydrates. It increases after digestion, and diminishes with fasting, disappearing altogether after an abstinence of four or five days. It will then reappear very rapidly after a meal of starchy or saccharine matters. From these facts it is apparent that glucose, when taken as food, or absorbed from the alimentary canal, is deposited in the liver under the form of glycogen. The change which takes place is a dehydration, as follows:

$$\begin{array}{ccccc} \text{Glucose.} & & \text{Water.} & & \text{Glycogen.} \\ C_6H_{12}O_6 & - & H_2O & = & C_6H_{10}O_5. \end{array}$$

While in this condition the glycogen forms part of the substance of the liver, and is probably a material of reserve, to be afterward consumed in some other part of the body. It appears to be gradually reconverted into glucose in the intervals of digestion, and to disappear under this form from the hepatic tissue.

Glycogen presents accordingly, in every respect, a strong analogy with vegetable starch. Its abundant presence in the embryonic organs, from which it disappears when they have acquired their growth, is like the deposit of starch in a seed, to be used up in the act of germination. And in the adult animal it is probable that a large portion, if not all, of the carbo-hydrates taken as food pass through the glycogenic condition before they are finally employed in the nutrition of the body.

Fats.

The fats form a well marked group of organic bodies which are widely diffused both in the vegetable and the animal kingdom. They are distinguished from the carbo-hydrates, first, by the fact that they do not contain hydrogen and oxygen in the proportion to form water, the oxygen being present in smaller quantity; and secondly, by their large proportion of carbon, which constitutes on the average a little over 75 per cent. of their weight. This fact is probably connected with their inflammability, the oils being oxidized at a temperature of 300° C., and burning with a bright flame. The smooth consistency of oleaginous matters is also one of their distinguishing features, and enables them to be employed as lubricating substances, to diminish the friction between opposite surfaces. In the pure condition they are destitute of taste and odor. They are all liquid at moderately high temperatures, and solidify by crystallization when cooled down to a certain point, which is different for each variety. The fatty substances which at ordinary temperatures have a thick, solid, or semi-solid consistency, are more especially designated as "fats;" those which are more liquid are spoken of as "oils." They have no rotatory action on polarized light. They are insoluble in water, and do not mix with it except by mechanical agitation; after which the two fluids separate from each other according to their specific gravity, the water remaining below and the oil rising to the surface in a distinct layer. Fats and oils are slightly soluble in alcohol, and freely soluble in ether, which is used to extract them from admixture with other organic substances.

Fatty matters are found in varying quantity in different vegetable tissues, the most abundant deposit occurring in nuts, fruits, and seeds, particularly those of the sweet and bitter almond, the chocolate tree, hemp, flax, Ricinus communis, and Croton tiglium, in which last it is in the proportion of 60 per cent. The seeds of plants generally are designated as "starchy" or "oleaginous," according to the preponderance of one or the other of these substances in their tissue. In the animal body, fat is most abundant in the adipose tissue and in the marrow of the long bones, where it amounts to from 80 to 96 per cent. In the human subject, under normal conditions, the entire quantity of fatty matters has been estimated at from 2.5 to 5 per cent. of the bodily weight.*

The following list gives the proportion of fat in various alimentary substances, according to the tables of Payen:

QUANTITY OF FAT IN 100 PARTS IN

Wheat	2.10	Beef's flesh (average)	5.19
Indian corn	8.80	Calf's liver	5.58
Potatoes	0.11	Mackerel	6.76
Beans	2.50	Salmon	4.85
Peas	2.10	Oysters	1.51
Sweet almonds	24.28	Cow's milk	3.70
Chocolate nut	49.00	Fowl's egg	7.00

Beside entering as an ingredient into the above articles, fat is often taken with the food in a pure, or nearly pure, form, as butter, olive oil, or adipose tissue.

Origin of Fatty Substances.—The first production of these organic

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*Gorup-Besanez: Physiologischen Chemie. Braunschweig, 1878, p. 169.

matters takes place in the act of vegetation, in all probability by a metamorphosis of starch or sugar already formed. This is the origin of fatty matters generally recognized by vegetable physiologists. In this change the proportions of carbon and hydrogen are increased 50 or 60 per cent., while that of the oxygen is largely diminished. By itself, accordingly, it would be a reducing process, similar to that by which starch is first formed from inorganic matter. But this is not the view usually entertained in regard to it. The deoxidation of carbonic acid and water can take place, so far as we know, only in the chlorophylle-holding cells of the plant; and fatty matter is often produced, as in oily seeds, where no chlorophylle is present. It is possible that the reduction of the quantity of oxygen, during the conversion of starchy matters into fat, may be accompanied by the liberation of carbonic acid, and the formation of other highly oxidized substances, which would account for the diminished proportion of oxygen remaining. Something of this sort takes place in the alcoholic fermentation of glucose, already described (page 57), as follows:

$$\underset{\text{Glucose.}}{C_6H_{12}O_6} = \underset{\text{Alcohol.}}{2C_2H_6O} + \underset{\text{Carbonic Acid.}}{2CO_2}.$$

Here the alcohol produced by fermentation contains a smaller proportion of oxygen than the original glucose; but another body (carbonic acid), containing a larger proportion, has been liberated at the same time. The missing oxygen therefore has not been discharged in the free condition, but in a more stable form of combination than before. A similar change taking place in the starchy or saccharine matters of a plant, with the production of fat, would not be altogether a deoxidation, but would include a rearrangement of the chemical elements, with the simultaneous production of other compound bodies.

There are no means at present known by which the transformation of starch into fat can be artificially accomplished, and even its chemical formula cannot be expressed with any reasonable certitude. But there are well-known facts which make it highly probable that such a change may be and is effected in the tissues of the living plant. In the first place, it is certain that starch disappears from the leaves in which it is produced, to be transported under a soluble form to other organs. Secondly, there are instances of the production of oily seeds, or other fatty reservoirs, in plants where no other deposit than that of starch can be detected in their chlorophylle-holding leaves.* And, thirdly, the oily seeds of certain plants while still immature contain starch, but as they ripen the starch diminishes or disappears and oil takes its place.†

Varieties of Fat.—The most important and abundant varieties of fat are *Stearine*, *Palmitine*, and *Oleine*. They resemble each other in general character, and differ mainly in their degree of consistency, stearine being the most solid at ordinary temperatures, while palmi-

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*Mayer: Agrikultur Chemie. Heidelberg, 1871. Band I., p. 86.

†Johnson: How Crops Grow. New York, p. 94.

tine holds an intermediate position in this respect, and oleine is the most fluid.

1. Stearine, $C_{57}H_{110}O_6$,

So called from the readiness with which it assumes the solid form, is a main ingredient of the more consistent fats. It liquefies at 66°.5 C., and again solidifies when the temperature falls below this point. It crystallizes, on cooling from a warm solution in oleine, in fine radiating needles, which often follow a wavy or curvilinear direction. It is rather less soluble in alcohol and ether than the other fatty substances.

2. Palmitine, $C_{51}H_{98}O_6$,

Was first recognized as an ingredient of *palm oil*, a semi-solid fat obtained from the seed of an African palm. It crystallizes, on cooling from its concentrated alcoholic or ethereal solution, in the form of slender needles. It liquefies at 60° C. It occurs abundantly in a variety of animal and vegetable fats.

3. Oleine, $C_{57}H_{104}O_6$.

As its name indicates, this is the representative ingredient of the *oils*, or liquid fatty substances. When pure it is transparent and colorless. It retains its fluidity at ordinary temperatures, and even below the freezing point of water. It readily dissolves both stearine and palmitine, its solvent power increasing with the elevation of the temperature.

Physical and Chemical Changes of the Fatty Substances.—There are certain changes of condition produced in the fats by external influences which are characteristic of these substances as a class. The first is that by which an oily substance, when mingled with a watery liquid, is reduced to the state of an *emulsion;* that is, a mixture in which the oil is broken up into minute particles and uniformly disseminated through the watery liquid. This change will not take place when oil is added to pure water, or to a watery solution of neutral or acid salts. But if a trace of alkali or alkaline carbonate be present, the fatty substance is at once disseminated throughout the mass, and held in permanent suspension. In such a mixture there is no change in the chemical characters of either the oil or the watery liquid, but only in their physical condition;—the two being retained in contact with each other in a state of minute subdivision. By evaporation the watery parts may be separated and the oil left behind unaltered. An emulsion formed in this way is whitish or white in color, and opalescent or opaque, according to the proportion of oily matter present. The emulsion of oil may also be accomplished by certain organic matters in watery solution, especially by the albumen of egg, or the albuminous ingredients of the blood and secretions. It is under this form that oily matters exist, when in considerable quantity, in the animal fluids, such as the milk, the chyle, or the blood.

Another change which may be produced in the fats is that of *saponification.* This is a chemical change in which the oily substance loses its original character, and its elements appear under new forms of combination. When an oily or fatty matter is kept for some hours at a high temperature in emulsion with water and an alkali, it is decomposed with the assimilation of the elements of water, producing a fatty acid and glycerine. The change which takes place is as follows:

STEARINE. WATER. STEARIC ACID. GLYCERINE.

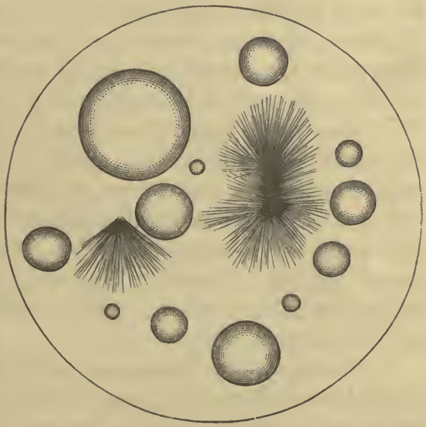
$$C_{57}H_{110}O_6 + 3H_2O = C_{54}H_{108}O_6 + C_3H_8O_3.$$

The acid product is stearic, palmitic, or oleic acid, according to the variety of fat used; and, when set free, it unites with the alkali, forming a neutral stearate, palmitate, or oleate. In such a combination the oil is said to be saponified, and in this form becomes more or less soluble in watery and serous liquids. Oil may be also decomposed by means of superheated steam, with the production of glycerine and free fatty acid, the latter of which is then easily saponified by either a caustic alkali or an alkaline carbonate.

There is some doubt whether the saponification of fat takes place in the animal body. Saponified fats are enumerated by some observers as constant ingredients of the blood-plasma, while their presence is denied by others. All agree that if present they are in extremely minute proportion, by far the larger quantity of fat retaining its chemical characters so long as it can be traced in the circulation.

Condition of Fatty Matters in the Living Body.—None of the fatty substances occur naturally in an isolated form, but they are mingled in varying proportions in all the ordinary animal and vegetable fats and oils. The consistency of the mixture varies with the relative quantity of its ingredients. The more solid fats, such as suet and tallow, consist largely of stearine; the softer fats, as lard, butter, and those of human adipose tissue, contain a greater abundance of palmitine; while the liquid fats, like fish oils, olive oil, and nut oil, are composed mainly of oleine. As a general rule, in the warm-blooded animals, these mixtures are fluid, or nearly so; for, although both stearine and palmitine, when pure, are solid at the temperature of the body, they are held in solution during life by the oleine with which they are associated.

FIG. 5.



OLEAGINOUS SUBSTANCES OF HUMAN FAT. Stearine and Palmitine crystallized; Oleine fluid.

As the body cools after death, the stearine and palmitine sometimes separate in a crystalline form, since the oleine can no longer hold the whole of them in solution. (Fig. 5.)

When in a fluid state the fatty substances present themselves in the form of drops or globules of various sizes, which may be recognized by their optical properties. They are circular in shape, with a well-defined outline. They often have a faint amber color, which is distinctly marked in the larger globules, less so in the smaller. As they are more highly refractive than the watery fluids in which they are immersed, they act as double convex lenses, and concentrate the light transmitted through them at a point above the level of the liquid. Consequently, they present the appearance of a bright centre surrounded by a dark border. If the lens of the microscope be lifted farther away, the centre of the globule becomes brighter and its borders darker. These characters will usually be sufficient to distinguish them from other fluid globules of less refractive power.

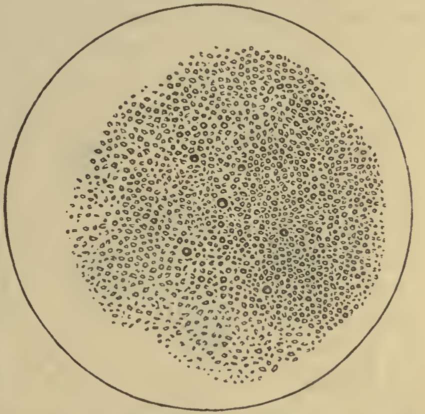
The oleaginous matters present a striking peculiarity in regard to the form under which they occur in the living body, and by which they are distinguished from the remainder of its ingredients. Instead of combining with the other constituents of the animal solids and fluids, in homogeneous union or solution, they are deposited, as a rule, in distinct masses or globules, suspended in the serous fluids, interposed between the anatomical elements, included in the interior of cells, or deposited in the substance of fibres or membranes. Even in the vegetable tissues, they are always in the form of drops or granules.

Owing to this fact the oils can usually be extracted by mechanical means. The tissues are cut into small pieces and subjected to pressure, by which the oil is forced out from the parts in which it was entangled, and separated, without further manipulation, in a state of comparative purity. A moderately elevated temperature facilitates the operation by increasing the fluidity of the oleaginous matter; but no chemical agency is required for its separation. Under the microscope, oil-drops and granules can be distinguished from the remaining parts by their optical properties and by the aotion of ether, which dissolves them, for the most part, without attacking other neighboring substances.

In the adipose tissue the oils are contained in the interior of vesicles, the cavities of which, in a state of health, they completely fill. The adipose vesicle, which varies in diameter, in man, from 28 mmm. to 125 mmm., is composed of a thin membrane, forming a closed sac, in which the oily matter is included. Sometimes, in cases of emaciation, the oil partially disappears from the cavity of the vesicle, its place being taken by a watery serum; but the serous and oily fluids remain distinct in the vesicular cavity.

In the chyle, the oleaginous matter is in a state of emulsion, and its subdivision is here more complete than anywhere else in the body. It presents the appearance of a fine granular dust, known as the "molecular base of the chyle." A few of its granules measure 2.5 mmm. in diameter; but they are generally much less than this, and the greater part are so small that they cannot be accurately measured. (Fig. 6.) For the same reason they do not present the brilliant centre and dark border of large oil-globules; but appear by transmitted light only as minute granules. The white color and opacity of the chyle, as of other fatty emulsions, depend upon this molecular condition of the oily ingredients. The albumen and salts, which are in intimate union with each other, and with the water, would alone make a colorless and transparent fluid; but the oily matters, suspended in distinct particles, with a different refractive power from that of the serous fluid, interfere with its transparency, and give to the mixture its diffused white color. The oleaginous nature of the particles is shown by their solubility in ether.

Fig. 6.

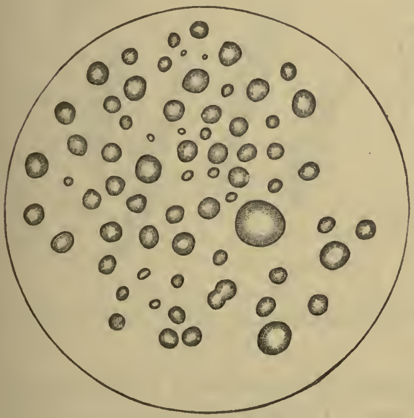


Chyle, from commencement of Thoracic Duct, from the Dog.

In milk the oily matter occurs in larger masses, or "milk-globules," which have an average diameter of 6 mmm. They are not quite fluid, but have a pasty consistency, owing to the large quantity of palmitine which they contain, as compared with the oleine; and under the microscope they present accordingly a somewhat irregular outline. By heating the milk they may be completely liquefied, and made to assume a globular form. When forcibly beaten into a mass by churning, they constitute butter.

In certain parts of the body oil-drops and granules are deposited in the substance of cells or other anatomical elements; as in the laryngeal, tracheal, and costal cartilages, and the secreting cells of the sebaceous glandules. Oily matter also occurs, under the same form, in the glandular cells of the human liver, where it is a constant ingredient in a state of health. In certain cases of disease it accumulates in excessive quantity, producing a fatty degeneration of the organ.

Fig. 7.

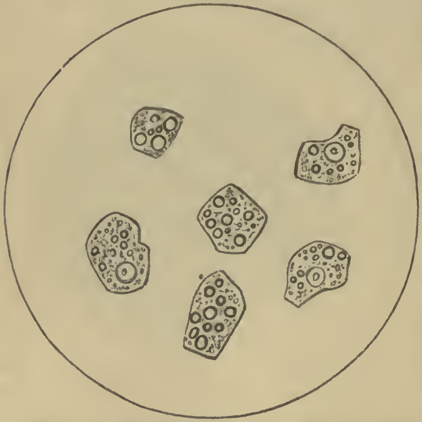


Globules of Cow's Milk.

In the carnivorous animals it exists normally in the epithelium cells of the convoluted portion of the uriniferous tubules. The drops and granules are here so numerous as often to fill, apparently, the whole calibre of the tubules.

In the marrow of the long bones it is more abundant than in any other tissue, occurring both inclosed in vesicles and in the form of free oil-drops. It exists in considerable quantity in the yellow wall of the corpus luteum. It is also deposited in the substance of muscular fibres under various conditions; in those of the voluntary muscles after prolonged disuse, those of the heart in fatty degeneration of this organ, and those of the uterus after delivery. In the uterine muscular fibres it makes its appearance soon after parturition, and continues to be present during the involution or resorption of the uterine tissue.

FIG. 8.



HEPATIC CELLS containing oil-globules. Human.

Source of Fat in the Animal Body.—It is evident from the composition of many nutritious substances consumed by man and animals that a considerable quantity of fat is introduced into the body with the food. The oleaginous ingredients of the cereal grains, of nuts and olives, of eggs, milk, and meat, show that both animal and vegetable foods contribute a certain proportion of fat to the system. But it appears that fatty substances may also be formed within the body, for under some conditions more fat is deposited in the adipose tissue and elsewhere than can be accounted for by that introduced during the same time with the food. This fact has been placed beyond question by the experiments of Dumas and Milne Edwards * on bees, those of Persoz on geese, those of Boussingault † on geese, ducks, and pigs, and those of Lawes and Gilbert ‡ on pigs. In these experiments the amount of fat in the whole body was first ascertained by comparative examination of other animals in the same condition. The subjects of the experiment

FIG. 9.

MUSCULAR FIBRES OF HUMAN UTERUS three weeks after parturition.

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*Annales de Chim. et de Phys. 3^{me} Série. tom. XIV., pp. 400, 408.

† Chimie Agricole. Paris, 1854.

‡ Philosophical Magazine. London, 1866. Vol. XXXII., p. 439.

were then kept upon a definite regimen, in which the quantity of fat was determined by analysis. This was continued for periods varying from one to eight months, after which the animals were killed and their tissues examined. The result showed that considerably more fat had accumulated in the system than had been supplied in the food. Consequently, oleaginous substances must in some cases, and perhaps habitually, be formed in the interior of the body by transformation of other nutritive materials. There is no discrepancy among observers on this point.

As for the special materials from which fat is thus produced in the animal system, its most probable source seems to be the carbo-hydrates. It has already been shown (page 63,) that such a change undoubtedly takes place in vegetables; and as it is not effected in plants, so far as we can judge, by simple deoxidation, but by a kind of process which may also take place in animals, there is no reason for doubting the possibility of a similar transformation in the interior of the animal body. Other considerations make it highly probable or certain. Vegetable-feeding animals, like sheep and cows, living on green food abounding in carbo-hydrates, will often accumulate a large amount of fatty matter in the system, or discharge it with the milk. In many of the experiments just quoted, the carbo-hydrates preponderated so much in the food supplied, that the excess of fat produced during the observation could hardly be attributed to any other source. And finally, it is a matter of common experience that food consisting of starchy and saccharine materials is especially a fattening food, both for the domestic animals and for man.

But these substances do not possess in themselves the requisite conditions for a fatty transformation; it can take place only in the living body. As the deoxidation of carbonic acid and water by plants is effected under the influence of their chlorophylle, so the carbo-hydrates of the food require the action of the animal tissues for their conversion into fat. This explains why the fat production varies so much under the same diet in different animals, and even in different individuals of the human species. There are cases of hereditary obesity, coming on at the same period of life in the children as in the parents, irrespective in great measure of the kind of food employed; and there are persons who seem hardly capable of taking starchy or saccharine substances without converting them into fat, while others may continue a mixed diet indefinitely without increasing their adipose tissue.

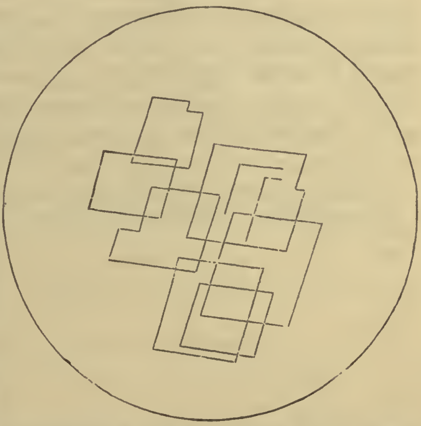
It is not unlikely that fat may also be formed from the albuminous matters of the food, though the evidence of this is less satisfactory than in the case of the carbo-hydrates. Carnivorous animals, as a rule, have less fat than the herbivora; and, among men, those who habitually consume a large proportion of meat are less liable to obesity than those living mainly on vegetable food. Nevertheless, it is believed by many that fat is sometimes the result of a partial decomposition of albuminous matters. In this case, the production of fat must be accompanied by the liberation of another substance containing nitrogen, which is an element in the composition of albumen. We know that this actually occurs in the living body, and that such a nitrogenous substance (urea) is discharged with the urine. Still this only gives a possibility, but not a proof, that the other product of decomposition is a fat. Furthermore, the appearance of fat in isolated drops and granules, in the substance of glandular cells or degenerating muscular fibres, of which we know so many instances, has been regarded as an indication that the fatty material in these cases is formed on the spot from the albuminous substance in which it is imbedded. But it is evident that the substance of the cell or muscular fibre is permeable to serous fluids containing saccharine ingredients, and that these may have been the immediate source of the fatty deposit. Most of the other reasons adduced in favor of the production of fat from albuminous matters are open to similar objections. On the whole, it may be said, that while we have no reason to discredit the possibility of a fatty transformation of albuminous matters, the main source of oleaginous substances, in point of fact, over and above those contained in the food, is to be found in the carbo-hydrates.

Physiological Relations of Fat.—The fatty substances of the body are subservient to a variety of uses. Some of these uses are of a physical character, while others imply chemical changes which are evidently of the first importance in nutrition, though as yet unknown in their details. The first and most palpable function of the adipose tissue is a mechanical one. It acts as a cushion to protect the neighboring parts from injury, and to facilitate the movement of muscular organs. The adipose layer in the subcutaneous tissue, in the soles of the feet and the palms of the hands, between the voluntary muscles, about the eyeball at the fundus of the orbit, and about the heart at the origin of the great vessels, is mainly useful in this way. The plicæ adiposæ of the articular cavities have a similar mechanical function, and the sebaceous secretion of the cutaneous glandules, by its oleaginous properties, protects the skin and hair from desiccation and preserves their pliability. The fatty tissue is also important as a non-conductor of heat. It envelops the subcutaneous parts like a blanket, and retains in the system much of the animal heat which would otherwise be dissipated. Its deposit in certain localities, as in the omentum, has no doubt a special reference to the protection, in this respect, of the underlying organs. In all these situations, however, the fat is an indifferent body in its chemical relations. Throughout the system, wherever fat can be recognized by the microscope in the form of distinct drops or globules, it is evidently, for the time being, in a state of physiological inactivity, being transported by the circulating fluids or retained on the spot as a nutriment of reserve. In certain parts, where it is very abundant, as in the marrow of the long bones, we can hardly attribute to it any further value than this. But it has also other functions immediately connected with the renovation of the tissues. This is shown by the fact that it is often taken with the food in noticeable quantity and consumed in the body, without any increase of the internal adipose deposit. In cases of acute wasting disease, of temporary abstinence, and in the hibernation of animals, the fat previously stored up greatly diminishes or disappears altogether. In these instances the oleaginous matter which disappears from the body is not to be found in the excretions. The sebaceous secretion of the skin is the only form of fatty matter discharged externally, and this is far inferior in quantity to that taken with the food and consumed by the system. The fat which thus disappears is therefore disposed of by decomposition in the body. We cannot follow with any certainty the steps of this decomposition, nor determine the successive alterations which take place in the fatty substance during its passage through the system. But it undergoes changes of some kind by which its essential characters are lost, and its elements are finally discharged under another form in the products of excretion.

Cholesterine, $C_{26}H_{44}O$,

So called from its occurring as a solid deposit from the bile, in which form it was first discovered. It is included in the present group of organic compounds, owing to its being crystallizable and non-nitrogenous. But it has no real affinity with the fatty matters, although it resembles them in certain physical properties, such as its insolubility in water, and its solubility in ether, boiling alcohol, chloroform, oily liquids, and solutions of the biliary salts. It is incapable of saponification, and at a high temperature (360° C.) may be volatilized without decomposition. Its solutions rotate the plane of polarization to the left 32°. It is deposited from its alcoholic or ethereal solution in the form of thin, colorless, transparent, rhomboidal plates, portions of which are often cut out by lines of cleavage parallel to the edges of the crystal. They frequently occur deposited in layers, in which the outlines of the subjacent crystals show very distinctly through the substance of those above. If the crystals be treated with a mixture of 1 volume of water and 5 volumes of sulphuric acid, and gently warmed, their borders take a bright carmine color, changing afterward to violet. (Gorup-Besanez.)

Fig. 10.



Cholesterine, from the contents of an encysted tumor.

If triturated with strong sulphuric acid, they yield, on the addition of chloroform, a blood-red color, which afterward disappears by exposure, passing gradually from red to violet, blue, and green, the liquid finally becoming colorless. (Hoppe-Seyler.)

Cholesterine is a constant ingredient of the bile, in which it occurs in the proportion of 0.5 part per thousand, and which seems to be its principal channel of exit from the system. It is also present in the sebaceous matter of the skin, and appears in considerable quantity in accidental deposits or exudations, such as biliary calculi, the fluid of hydrocele, and the contents of various encysted tumors. It exists in the blood, the liver, the spleen, the crystalline lens, and especially in the nerves, spinal cord, and brain, in which last it has been found by Flint* in the proportion of about one part per thousand. It is also present in the yolk of egg, and in the spermatozoa of all the higher and lower animals.† It is not confined to the animal body, but is found in many vegetable structures, such as wheat, Indian corn, peas and beans, olives, almonds, young buds, and mould-fungi.

The physiological relations of cholesterine are very obscure, as compared with those of true fatty substances. Notwithstanding its wide distribution in the animal system, in nutritious substances, in the blood, and in such important organs as the brain and nerves, it is mostly regarded as a product of decomposition of their organic ingredients, rather than as serving for the nutrition of the tissues. But from what substance it is derived, or in what way it is produced, is at present unknown. It seems to be, without doubt, absorbed from the substance of the nervous system by the blood, transported in this way to the liver, and thence discharged with the bile into the alimentary canal. In the observations of Flint,* its quantity in the blood of the dog was found to increase while passing through the brain, from 0.52 to 1.09 per thousand parts. Its presence in the blood, as a product of organic disintegration, would explain its frequent occurrence in exudations and morbid deposits in different parts of the body. According to most observers (Lehmann, Gorup-Besanez, Hoppe-Seyler) it is a normal ingredient of the feces, as well as of the sebaceous matter, and is therefore either wholly or partly discharged from the body under its own form.

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* American Journal of the Medical Sciences. Philadelphia, October, 1862.

† Hoppe-Seyler. Physiologische Chemie. Berlin, 1877, p. 81.

CHAPTER IV.

ALBUMENOID SUBSTANCES.

THE albumenoid substances as a class occupy the first place in importance in the living body. Their wide distribution, their abundant quantity, and the part which they take in the vital operations indicate a marked distinction between them and all other ingredients of the organized frame. They are derived both from animal and vegetable sources, and none of the nutritious juices in either kingdom is without them. But in plants, as a rule, the albumenoid substances are in comparatively small quantity, while in man and animals they are by far the largest part of the solid constituents of the body, and with the exception of water are more abundant than any other of its ingredients. In the blood and muscles they form nearly 20 per cent. of the whole mass, and in the bones and cartilages from 30 to 40 per cent. Many of them have special forms of activity which distinguish them from all other organic substances; and everywhere their chemical constitution, their physical characters, and their physiological properties show them to be directly connected with the active phenomena of life.

General Characters of the Albumenoid Substances.—The first important feature of these substances is that they contain nitrogen as one of their constituent elements. This at once distinguishes them from the preceding group, and gives them a different place as ingredients of the food. The quantity of nitrogen present varies from about 14 to 18 per cent. of their weight. Most of them contain also a small quantity of sulphur, and nearly all, when incinerated, leave a minute residue of lime phosphate, from which they cannot be entirely freed by the usual means of purification. Their average composition by weight, according to the tables of Hoppe-Seyler, Wurtz, and Gorup-Besanez, is as follows:

Average Composition of Albumenoid Substances.

Carbon	52.8
Hydrogen	7.1
Nitrogen	16.6
Oxygen	22.1
Sulphur	1.4
	100.0

Their exact chemical structure has not been determined with certainty in any case. Owing to the difficulty of obtaining them in a state of absolute purity, the uncertainty whether their sulphur is an essential constituent element or only an incidental ingredient, and particularly owing to the number and variety of the products of their artificial decomposition, their atomic constitution is still a matter of doubt. The formula for albumen which was proposed by Lieberkühn, and adopted by Johnson and Schützenberger,* is as follows:

Albumen; $C_{72}H_{112}N_{18}O_{22}S$.

But although this formula has been shown to account in a satisfactory manner for certain combinations and decompositions, it has not been generally accepted; and in the opinion of most chemists, the manner in which the elements of these substances are combined is entirely unknown.

The albumenoid matters are not crystallizable. They always, when pure, assume an amorphous condition, in which they are sometimes solid, as in the bones; sometimes fluid, as in the plasma of the blood; and sometimes semi-solid, as in the muscles and the glandular organs. Even in the fluids, when present in considerable quantity, as in the blood-plasma, the pancreatic juice, or the submaxillary saliva, they give to the solution a viscid or mucilaginous consistency, which is more marked in proportion to their abundance.

Some of them are soluble in water, others in solutions of the neutral salts in different degrees of concentration. Some of them may be extracted from the solid tissues by water at a boiling temperature, and a few resist the action of all solvent fluids. When in solution they all rotate the plane of polarization toward the left. They are all hygroscopic. When dried by evaporation, and afterward brought in contact with water, they absorb it with readiness, becoming swollen and assuming a more or less softened, gelatinous, mucous, or fluid consistency, according to the quantity of water with which they were originally associated. When subjected to artificial decomposition by heat and a caustic alkali, they yield a great variety of gaseous and crystalline substances, among which carbonic acid and ammonia are constantly present in the proportion of 2 to 1.† Oxalic acid and sulphurous acid are also given off as products of decomposition.

The albumenoid substances are *not diffusible;* that is, they do not readily pass, in solution, through parchment paper or animal membranes. This character is probably connected with their amorphous and uncrystallizable condition; and they are distinguished by it in a marked degree from mineral salts and crystallizable organic substances, which pass through such membranes by diffusion with great facility. It is frequently resorted to as a means for the purification of albume-

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* Wurtz. Chimie Biologique, Paris, 1880, pp. 65, 85.

† Gorup-Besanez. Lehrbuch der Physiologischen Chemie, Braunschweig, 1878, p. 114.

noid substances from other matters with which they are mingled. Thus if a solution containing albumen, glucose, and sodium chloride be immersed in a vessel of pure water, with a partition of parchment paper between the two liquids, the glucose and the salt will pass through the membrane and become diffused in the water, while the albumen will remain behind. By renewing the water in the exterior vessel and thus keeping up the activity of diffusion, nearly the whole of the glucose and the salt may be removed from the interior solution, and the albumen left in a purified condition. This method is termed "dialysis," and is frequently employed for obtaining albumenoid matters free from admixture with other substances. There is one remarkable exception, among the albumenoids, to the rule of non-diffusibility. It is that of "peptone," the substance produced from albuminous matters by digestion, which retains all their other essential properties, but has acquired the power of passing by diffusion through animal membranes. It is thus rendered capable of being absorbed by the intestine, and of entering the current of the circulation.

The albumenoid substances are *coagulable.* This property consists in their capacity, when fluid, of suddenly changing, under certain physical or chemical influences, to the solid form; so that they either separate from the other ingredients of the liquid, or convert the whole into a gelatinous mass. This difference depends on the relative quantity in which they are present, and on the manner in which they are associated with the other ingredients. Thus if a specimen of slightly albuminous urine be heated, the albuminous matter is thrown down as a flaky deposit, while the rest remains liquid; but if the serum of blood be treated in the same way it solidifies into a uniform mass. In neither case is the process of coagulation a simple precipitation, as where a mineral salt is thrown down from solution in a fluid. The albumenoid substance, when coagulated, still retains its normal proportion of water, and in the instance of the serum of blood, it holds the whole of the water present, so that no liquid separates from the coagulum. It may be driven off by evaporation, but the coagulated albuminous matter is still hygroscopic, and will again take up water by absorption to the same extent as before. A coagulated substance is usually permanently altered in character, and cannot be restored to fluidity except by means of acid or alkaline solvents, which still further modify its original properties.

Different albumenoid matters are coagulated by different agents, and these reactions form a convenient and sometimes the principal test by which they are distinguished. Thus albumen is coagulated by heat or the mineral acids, but not by organic acids. Caseine, the albuminous ingredient of milk, is coagulated by either mineral or organic acids, but not by heat. The animal matter of the pancreatic juice is coagulated by heat or the mineral acids; but also by magnesium sulphate, which does not affect albumen. The coagulation of some albumenoid matters is caused by the action of ferments, which are without influence on the remainder. The exact nature of the change which takes place in coagulation has not been determined, and it probably cannot be successfully investigated until the real constitution of the albumenoid substances is known.

Another important feature of the albumenoid substances is their connection with "catalyses" or "catalytic transformations." These are chemical changes, either combinations or decompositions, which take place under the influence of a body acting in a hitherto unexplained way, apparently by mere contact and without being itself either decomposed or combined. Such a body is a *ferment.* It produces its effect in very small quantity; and it may cause important transformations in a large amount of other material without its own substance being perceptibly diminished. Thus the starchy matter of plants is converted into glucose by the influence of a nitrogenous body termed "diastase;" and according to Payen,* one part of diastase is capable of converting into glucose 2,000 parts of starch. All the ferments belong to the class of albumenoid substances. Many of these substances are themselves liable to catalytic transformation under the influence of ferments. Such transformations are certainly the principal acts in the digestion and assimilation of food; and changes of a similar kind are so general and so important throughout the body that some physiologists are inclined to attribute to their influence all the essential phenomena of nutrition and waste. Each ferment operates with the greatest vigor under certain special conditions; as, for example, an acid, neutral or alkaline medium, the presence or absence of a saline solution, or a slightly higher or lower temperature; but they are all arrested by the strong acids or alkalies, by concentrated saline solutions, by the absence of moisture, or by a boiling or freezing temperature. The most favorable temperature is usually about that of the living body.

At a temperature of 300° C. or over, the albumenoid substances are decomposed into gaseous products. But if subjected for a certain time to a temperature of about 125° C., they undergo a change by which a peculiarly agreeable flavor is developed, and by which many of them become suitable for human food. It is this flavor which is produced in the process of *cooking*, and which always depends upon the presence of a certain quantity of albumenoid matter in the substance employed. If the temperature at which the cooking process is carried on be too low, the characteristic flavors are not developed; if it be too high, they are destroyed and replaced by empyreumatic odors, from the combustion or decomposition of the ingredients of the food.

Lastly, the albumenoid substances are distinguished by the property of *putrefaction.* This is a process in which dead animal substances, when exposed to the atmosphere at a moderately warm temperature,

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* Substances Alimentaires, Paris, 1865, p. 5.

soften, liquefy, and are finally decomposed, with the production of certain fetid gases, among which are hydrogen sulphide and carbide, usually with more or less carbonic acid, nitrogen, and ammonia. These emanations cause an odor which is easily recognized as "putrefactive;" and no substance is capable of putrefaction, unless it contain albumenoid matters among its ingredients. As these matters are more abundant in animals than in vegetables, the phenomena of putrefaction are most distinctly marked in the decay of animal tissues. But they will take place in both, under the requisite conditions. The rapidity of putrefaction in animal substances varies with their consistency; the liquids and the soft parts undergoing this change more readily than those of firmer texture. In some which are exceedingly dense, like the bones, cartilages, hair, and elastic tissues, desiccation may take place before putrefaction can be established; but if their animal matter be extracted in the form of gelatine or otherwise, and kept for a short time in the moist condition, it will putrefy like any other albumenoid substance.

In order that putrefaction may take place, certain conditions are necessary. In the first place, it requires the access of atmospheric air, or of some fluid containing oxygen. If the putrescible substance be boiled, so as to expel all the free oxygen contained in its fluids, and inclosed in a hermetically sealed vessel, no putrefaction takes place, and the substance remains unaltered indefinitely. It is by this means that cooked meats are preserved in cans, for use upon long voyages or expeditions. So long as the cans are kept perfectly closed, their contents remain sound. After they are opened and the air admitted to their interior, the food must be used at once, otherwise it will putrefy in a short time.

Another essential condition for putrefaction is the presence of moisture. Albumenoid substances in a perfectly dry state do not undergo decomposition; and in some regions, where a high temperature and a dry atmosphere favor their rapid desiccation, this fact is utilized for the preservation of meats. Immediately after the animal is killed, the flesh is cut into strips and dried in the air; and desiccation being thus completed before putrefaction has commenced, the food is preserved for future use.

The third requisite for putrefaction is a moderately elevated temperature. It goes on most rapidly between 25° and 35° C. Below 25° it gradually diminishes in activity, and ceases altogether about the freezing point of water. Meats, therefore, which are kept at a sufficiently low temperature do not putrefy. The carcass of an extinct mammoth has even been found imbedded in ice in Northern Siberia, in such a state of preservation that its flesh was devoured by dogs and other animals.* A temperature much above 35° is also unfavor-

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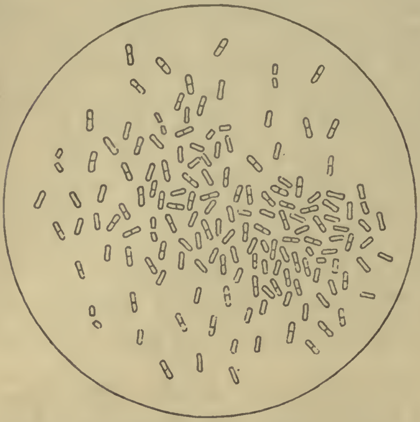
* Mémoires de l'Académie Impériale des Sciences de St. Petersbourg, tome 5, p. 440.

able to the putrefactive change, and it is completely arrested by a heat approaching that of boiling water.

Fig. 11.



Cells of Bacterium Termo; from a putrefying infusion.

The process of putrefaction is accomplished by the growth and multiplication of a microscopic vegetable organism, somewhat analogous to that causing the alcoholic fermentation in saccharine liquids. If any clear solution containing animal or vegetable albumenoid matters be exposed to the air at a moderate temperature, after a short time it becomes turbid. This turbidity is due to the development of minute vegetable cells, of very simple organization, which rapidly multiply in the decomposing liquid. The cells belong to the genus "Bacterium," so called from their rod-like form; and the species found in putrefying infusions is known by the name of *Bacterium termo.* The cells are of an oblong form, about 3 mmm. in length by 0.6 mmm. in thickness. They usually appear double, each pair consisting of cells placed end to end. This appearance is due to their multiplication by spontaneous division of the growing cell. After a time the two cells, thus formed out of a single one, separate from each other, and each repeats the process for itself.

One of the most remarkable characters of bacterium cells is their movement. During a certain period of their development they exhibit an incessant motion, consisting in a conical rotation about their longitudinal axis, by which they are transported in various directions. This motion is often so rapid that it can hardly be followed by the eye; in other instances it is so slow that its mechanism may be distinguished. The movement and multiplication of the cells go on while putrefaction continues. When all the albumenoid ingredients of the infusion have been decomposed, the liquid again becomes clear, and the bacterium cells subside to the bottom in a quiescent layer. But a small portion of this layer will readily excite putrefaction in another albuminous liquid.

As the bacterium cells effect the decomposition of albumenoid matters by means of their vegetative activity, putrefaction is limited by the same conditions. Bacteria belong to the group of colorless cryptogamic plants. Like other plants of this kind, they assimilate organic substances ready formed, at the same time absorbing oxygen and exhaling carbonic acid, after the manner of animals.

As oxygen therefore is essential to their growth, its presence is also necessary for putrefaction. Furthermore, as no plants can grow without moisture, and as they require a temperature of moderate warmth, putrefaction must also be suspended both by desiccation and by excessive cold or heat.

Fermentation and putrefaction, accordingly, are analogous processes, going on under the influence of different microscopic vegetations. The former takes place in saccharine liquids, the latter in those containing albumenoid matter; since the yeast-plant requires for its growth a preponderance of carbo-hydrates, while bacterium cells are nourished by the absorption of nitrogenous matter.

Origin of the Albumenoid Substances.—Albumenoid matters are first produced in the vegetable world by assimilation of nitrogen with the carbo-hydrates. This is proved by the fact that green plants which can produce starch and sugar from carbonic acid and water, if supplied with moisture containing nitrogenous salts, will thrive vigorously and increase many fold their contents of albuminous matter.* The production of this new material will take place in other parts of the plant beside the leaves, provided there be present saccharine juices already formed and nitrogen compounds fit for absorption. Furthermore, colorless plants, which cannot produce starch or sugar for themselves, if nourished with saccharine solutions and inorganic nitrogen compounds, will also largely increase the mass of their albumenoid ingredients.

It appears that the nitrogen thus assimilated by plants is not absorbed in a free state. Notwithstanding the abundant quantity of this element in the air, it is accepted by vegetable physiologists, as the result of decisive investigations, that the free atmospheric nitrogen is not available for vegetation.† Plants appropriate their nitrogen, both from the atmosphere and the soil, in the form of nitrates and ammonium salts, which are absorbed by the roots, taken up by the vegetable juices, and thus serve for the production of albumenoid substances. The sulphur requisite for these matters is taken up in the form of sulphates, which are afterward decomposed in the vegetable juices.

Classification of the Albumenoid Substances.—The arrangement of these matters in groups, according to appropriate generic characters, is necessary to facilitate their study and description. Attempts at such a classification, based upon their intimate chemical structure, must be futile, so long as we are destitute of certain knowledge in this respect. Even their characters of solubility in water, dilute acids or alkalies, or saline solutions, vary in different cases by such slight gradations that they can only be considered as convenient methods of diagnosis rather than as positive distinctions. Their treatment by stronger reagents yields substances which may be of interest for theoretical chemistry, but which are not to be found in the living body, and have no physio-

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* Mayer, Lehrbuch der Agrikultur-Chemie, Heidelberg, 1871, Band i. pp. 145, 150.

† Hoppe-Seyler, Physiologische Chemie. Berlin, 1877, p. 48.

logical value. The most serviceable arrangement for the study of these substances, as materials of the organized fabric, should include their simplest and most easily recognized physical characters, the forms under which they occur in the animal frame, and the part which they play in its vital operations. For this purpose they may be divided, as follows, into three principal groups.

ALBUMINOUS MATTERS.

These are the substances which naturally stand at the head of the albumenoid class. They were, many years ago, called "proteine-compounds," because Mulder, according to a view now abandoned, considered them as so many combinations of the same primitive body, "proteine," with varying proportions of sulphur and phosphorus. They are still designated by some writers as "proteids." They are all abundant ingredients of the nutritive juices, and their especial office in the living body seems to be the supply of material for the nourishment of the permanent structures. They include the following:

1. Albumen of Blood.

This substance, also called *Serum-albumen* or *Serine*, is the most abundant organic ingredient of the blood-plasma, where it exists in the proportion of 53 parts per thousand. After spontaneous coagulation of the blood, and separation of the clot and serum, it remains fluid in the serum. It is also found in the lymph, the chyle, the pericardial fluid, and in many pathological serous exudations. It is obtained from dilute serum by precipitating other albumenoid ingredients with acetic or carbonic acid, evaporating the filtered fluid to dryness, dissolving in water, and lastly removing its saline substances by the process of dialysis (page 75). Serum-albumen is soluble in water and in solutions of the neutral salts, from which it is not precipitated by either dilute alkalies or organic acids. Its watery solution is neutral in reaction, and rotates the plane of polarization toward the left 56°. It is coagulated by heat (72° C.), by the mineral acids, the metallic salts, and especially by potassium ferrocyanide in acidulated solution, which is the most delicate known test of its presence. It is coagulated by alcohol in excess, but not by ether. Its coagula are redissolved by the caustic alkalies.

2. Egg-albumen.

This is the main ingredient in the white of egg. It was the earliest studied of all the albumenoid matters, and received its name from the fact of its turning white and opaque when boiled. It is an important article of food, and supplies most of the albumenoid matter for the nourishment of the embryo chick during incubation. It is soluble in water and in neutral saline solutions. Its specific power of rotation for polarized light is 35.5°. Like serum-albumen, it is coagulated by heat, alcohol, mineral acids, metallic salts, and potassium ferrocyanide in acidulated solution; but it is also thrown down by agitation with ether, which does not affect the preceding variety.

3. Caseine.

Caseine is the albuminous matter of milk, where it is present in the proportion of a little more than 40 parts per thousand. It is insoluble in pure water and in neutral saline solutions, but soluble in slightly alkaline liquids. In liquids containing an alkaline phosphate, like milk, it remains in solution notwithstanding the alkaline reaction be neutralized (Hoppe-Seyler). It is not affected by a boiling temperature, but coagulates by most of the other agents which have this effect on albumen, namely, by the mineral acids, the metallic salts, and alcohol. It is furthermore thrown down by the organic acids and by magnesium sulphate, both of which are without action on albumen. Its specific rotary power for polarized light is greater than that of any other albuminous matter, amounting to 80°. Its most remarkable property is that of coagulating by contact with rennet, or the extract of the calf's stomach. Coagulated caseine forms the albuminous ingredient of cheese, whence its name is derived. When milk is taken as food it is coagulated in a similar way, in the stomach, by the ferment of the gastric juice. Caseine, in its various forms of preparation, is an abundant and important nutritious material.

4. Paraglobuline.

This substance is a constituent of the blood-plasma, where it exists in the proportion of 22 parts per thousand, being a little less than one-half as abundant as the albumen. After coagulation of the blood it remains, together with the albumen, as an ingredient of the serum. Its name is derived from the fact that it has similar, but not identical, reactions with a substance formerly extracted from the blood-globules, and by Lehmann termed "globuline;" one of the most prominent of these reactions being its precipitation from dilute blood-serum or saline solutions by a stream of carbonic acid, or by the addition of very dilute acetic acid. Paraglobuline belongs to a group of substances, including the two following, which are insoluble in pure water, but soluble in dilute solutions of sodium chloride, in which they are coagulable by heat. If the serum of the blood, accordingly, be subjected to a boiling temperature, the whole of its albumen and paraglobuline coagulate together; but if it be diluted with ten times its volume of water, and then treated with a stream of carbonic acid, its paraglobuline will be thrown down, while the albumen remains behind. Paraglobuline is also precipitable from blood-serum by the addition of powdered sodium chloride in excess.

The physiological relations of paraglobuline with albumen are unknown. The similarity in properties and quantity of the two substances, as ingredients of the blood, make it possible that either one may be a product of metamorphosis from the other; or they may both have been formed out of some other preceding substance, to serve for different purposes in the act of nutrition.

5. Fibrinogen.

This substance exists in a fluid form in the blood of the living body, and at the time of its coagulation is converted into fibrine. It is present in the blood in much smaller quantity than its other albuminous ingredients, amounting to not more than 3 parts per thousand. Like paraglobuline, it is insoluble in water, but soluble in neutral saline solutions, and in this condition is coagulable by heat. It is also thrown down from fluids which contain it by a stream of carbonic acid, or by dilute acetic acid. Its most striking character is its liability to coagulate by contact with a special ferment, the so-called "fibrine-ferment," which is considered as the natural exciting cause of its coagulation. This process is analogous to the coagulation of caseine by rennet; the fibrine-ferment acting only by contact, while the fibrinogen supplies the material of the solidified fibrine. If pure fibrinogen, in a dilute saline solution, be coagulated by heat, the quantity of coagulum so obtained is as great as that produced from coagulation by action of the ferment (Fredericq). This shows that the spontaneous coagulation of fibrinogen in the blood does not depend upon its union with another substance, but that it is simply a change of molecular condition, like that which occurs in other coagulable substances.

Fibrinogen is best obtained from horse's blood, according to the method of Hammarsten.* The blood, as it escapes from the vessels, is received into $\frac{1}{3}$ of its volume of a saturated solution of magnesium sulphate, with which it is thoroughly mingled. This arrests its coagulation. The mixture is then slowly filtered, to separate the blood-globules, and the clear filtered fluid is treated with its own volume of a saturated sodium chloride solution. This throws down the fibrinogen with some other albuminous matters. To effect its purification, the precipitate is cleansed from the adherent liquid by pressure with bibulous paper, finely divided, dissolved in a sodium chloride solution of the strength of 8 per cent., and again precipitated by the same salt in saturated solution. This operation is once more repeated; and after the third precipitation with saturated sodium chloride solution, the fibrinogen is redissolved in pure water. It is then in a state of purity.

Fibrine, produced by the coagulation of fibrinogen, is a tenacious whitish substance, of firmer consistency than coagulated albumen. It has a considerable degree of extensibility and elasticity, and will retract with sufficient force to gradually expel any surplus liquid entangled in it. It is insoluble in water and in neutral saline solutions. It is swollen and softened, but not liquefied, at ordinary temperatures, by dilute acids, and is slowly dissolved by dilute alkalies. If heated in contact with moisture, or treated with alcohol, it is rendered opaque, loses its extensibility and elasticity, and becomes in appearance more like coagulated albumen. It forms the solidified portion of inflammatory exudations on serous surfaces or in the tissue of diseased organs.

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* Archiv für die gesammte Physiologie. Bonn, 1879, Band XIX., p. 563.

6. Myosine.

The contractile substance of the striped muscular fibres during life consists largely of a thickish fluid or semifluid alkaline plasma. After death it coagulates, and the coagulating substance, termed "myosine," presents some analogy with the fibrinous matter of the blood. Its spontaneous coagulation gives rise to the condition of cadaveric rigidity, in which the muscular fibres lose their power of contraction and relaxation, becoming solidified and opaque. At the same time the reaction of the muscular tissue changes from alkaline to acid.

The coagulation of the muscular plasma, like that of the blood, is retarded for a time by the action of cold; and it takes place less rapidly, after death, in the cold-blooded than in the warm-blooded animals. This fact has been used by Kühne for its extraction, from the muscular tissue of frogs, in a liquid condition. The vascular system is first deprived of blood by an injection of a one-half per cent. solution of sodium chloride. The muscles, thoroughly washed, are then subjected for two hours to a temperature of 7° to 10° C. below the freezing-point, reduced to a pulp in a cold mortar, and then allowed gradually to thaw upon a filter. As the temperature rises the filtered fluid coagulates.

Coagulated myosine is a gelatinous amorphous substance, insoluble in water and in concentrated solutions of sodium chloride; but is dissolved by a watery solution of salt, made in the proportion of ten per cent. or less. It may be extracted after death by bruising the muscular tissue to a pulp in a ten per cent. solution of sodium chloride, filtering the expressed liquid, and allowing it to fall by drops into a large quantity of distilled water, when the myosine separates by precipitation. It is distinguished from coagulated fibrine by its solubility in neutral saline solutions of a certain strength, as well as by its ready solubility in feebly acidulated solutions. When dissolved in a neutral saline fluid it is coagulable by heat, like the albumen of blood.

7. Syntonine.

Syntonine is so called because formerly supposed to be the contractile ingredient of muscular flesh, from which it was obtained by extraction with a dilute acid. But a substance having the same characters may be extracted by similar means from many of the animal solids and fluids. Any one of the albuminous matters, if treated with a solution of hydrochloric acid of about 4 parts per thousand, after a time dissolves and becomes altered in its properties, so that it is soluble in either dilute acids or alkalies, but insoluble in neutral watery liquids and saline solutions. Its solution in a dilute alkali is coagulable by heat, and if previously boiled in water it becomes insoluble in dilute acids. It appears to be identical in character, from whatever source it is derived.

Obtained by the above means, syntonine is an artificial product. But the same substance is formed in the stomach during digestion by the action of the acid gastric juice upon the albuminous elements of the food. It is the first stage in the digestive process, by which all these substances are reduced to the form of syntonine. It may be precipitated from its solution in the gastric juice by careful neutralization with an alkali. This is the only situation in the body in which syntonine is known to be normally present.

8. Peptone.

This substance is the final product of the stomach digestion of albuminous matters. These matters, first converted into syntonine by the acid of the gastric juice, are further transformed by the action of its ferment or "pepsine." The result of this transformation is peptone; and it appears to be essentially the same substance, whether derived from the digestion of coagulated albumen, fibrine, myosine, or other nutritious albumenoids. It is soluble in water, in dilute acid and alkaline liquids, and in neutral saline solutions in all proportions. Even strong mineral acids have no effect upon it. It is not coagulated by heat, nor by potassium ferrocyanide in acidulated solution, a reagent so prompt and effective for albuminous matters in general; though it is thrown down by alcohol in excess and by the metallic salts. It has therefore acquired, in comparison with other substances of this group, an increased range of solubility.

But its most distinctive feature is its diffusibility. Unlike other albuminous matters, it passes readily through animal membranes or parchment paper. Comparative experiments on the two substances show that the diffusibility of peptone is about twelve times as great as that of albumen. By this means it is enabled to leave the cavity of the alimentary canal, and to pass through the walls of the blood-vessels into the circulation.

The transformation of albuminous matters into peptone is a phenomenon of catalysis. It does not represent any fundamental change in the chemical composition of these bodies, since the elementary analyses of peptone, thus far made, show that it contains nearly the same proportions of carbon, hydrogen, nitrogen, oxygen, and sulphur as the substances from which it is produced. The principal modification which takes place seems to consist in the assumption, by the original albuminous matter, of the elements of water,—that is, in a hydration. This is claimed as proved by direct experiment; and it is held by observers of high repute,* that peptone is simply an albuminous substance in its state of maximum hydration, retaining its chemical qualities and nutritive value, but altered in its physical properties of solubility and diffusibility. If this view be correct, peptone will stand in its relation to albumen very much as glucose in its relation to glycogen and starch.

The fresh juices of growing plants, and especially of the succulent vegetables, contain a nitrogenous substance coagulable by heat, and

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* Hoppe-Seyler, Physiologische Chemie. Berlin, 1878, p. 227.

corresponding with albuminous matters in chemical composition. It is known as "vegetable albumen." In peas and beans there is also a substance, termed "legumine," similar to the caseine of milk. It is not coagulated by heat, but is thrown down both by the organic acids and by magnesium sulphate in excess. According to some observers it is also coagulable by rennet. The cereal grains, and especially wheat, contain a substance insoluble in water, which, in its tenacity, extensibility, and elasticity, resembles coagulated fibrine. It is this substance which gives consistency to the dough made from wheaten flour, enabling it to retain the starchy materials in a consistent mass.

FERMENTS.

The substances belonging to this group are distinguished from the preceding; First, by their inferior quantity. Their amount is usually too small to allow either of exact chemical analysis or quantitative determination; and they are known more from their effects than from their physical characters. Secondly, their action is one of catalysis. They do not directly form the materials of nutrition, but they cause in these materials the changes requisite for assimilation. For this reason they are not perceptibly consumed in the process; a very small quantity of the ferment being sufficient to produce the needed result in a large quantity of material. Thirdly, when heated, in watery solution, to the boiling point, their properties are changed and they become inactive as ferments. This fact, which is denied by some writers, has been unmistakably evident in our own observations, and appears to be amply confirmed by the experience of others.* Fourthly, the ferments are precipitated from their solutions by alcohol in excess. But there is a marked difference, in this respect, between them and the albuminous matters proper. An albuminous matter, coagulated by alcohol, is permanently altered, and cannot be again rendered soluble except by means which still further modify its character. A ferment, on the other hand, when thrown down by alcohol, may be kept in this condition for an indefinite time; and, after the removal of the alcohol, if redissolved in water, will again exhibit its characteristic activity. The ferments may also be extracted and preserved by the action of glycerine, which is often used as a convenient means for their preparation.

1. Ptyaline.

This is a ferment belonging to human saliva, which has the property of converting boiled starch into sugar. Its action takes place most readily in a slightly alkaline solution, at the temperature of the living body. It is obtained in comparative purity by adding to the saliva dilute phosphoric acid, and neutralizing the solution with lime-water. The precipitate of lime phosphate thus produced brings

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* Hoppe-Seyler, Physiologische Chemie. Berlin, 1878, p. 113. Gorup-Besanez, Lehrbuch der Physiologischen Chemie. Braunschweig, 1878, p. 504. Ewald, Die Lehre von der Verdauung. Berlin, 1879, p. 122.

down with it the ptyaline, which may afterward be dissolved in water, precipitated by alcohol from its watery solution, and again dissolved in water. Evaporated to dryness, it is an amorphous nitrogenous substance, and when heated to decomposition, gives off the odor of burnt horn. It appears to be constantly present in human saliva, within a short time after birth, and in that of the gnawing animals, as rabbits and guinea-pigs; but is not found in that of the dog or horse.

2. Pepsine.

Pepsine is the digestive ferment of the gastric juice, by which the albuminous matters of the food are transformed into peptone. It operates only in an acidulated solution, since the influence of an acid is necessary for the preliminary conversion of albuminous matter into syntonine. It requires also a moderately elevated temperature, that of the living body being most favorable. Pepsine is prepared from gastric juice, according to the method of Schmidt, by neutralizing the fresh juice with lime-water, evaporating the filtered liquid to a syrupy consistency, and precipitating with absolute alcohol. The precipitate is redissolved in water, again thrown down by chloride of mercury, and the metallic precipitate decomposed by sulphuretted hydrogen. The filtered fluid contains pepsine in solution.

It is also obtained from the mucous membrane of the pig's stomach, which is cut into small pieces and digested for several days with glycerine. The glycerine extract is then treated by a large addition of alcohol, and the pepsine, thus precipitated, after being washed with alcohol, is dissolved in water. The solutions obtained by these processes are not supposed to contain the ferment in a perfectly pure state; but if slightly acidulated, they will exhibit its digestive action on albuminous matters at the temperature of the body with considerable energy. Pepsine is a non-diffusible substance, soluble in water and in glycerine. It is not precipitated by the mineral acids. It exists, with essentially the same properties, in the gastric juice and gastric mucous membrane of all animals hitherto examined, and is found in the stomach of the human embryo as early as the beginning of the fourth month.

3. Pancreatic Ferments.

In the secretion of the pancreas there are, beside a certain quantity of albuminous matter, no less than three ferments, differing in their mode of action. The most important of these is "pancreatine," or the sugar-producing ferment. It acts in a similar manner to ptyaline, but with greater energy; being, according to all observers, by far the most prompt and effective of all known substances for the conversion of starch into sugar. It is obtained by digesting the chopped pancreas in lime-water, after which the solution is neutralized by phosphoric acid, producing a precipitate of lime phosphate, by which the ferment is thrown down, entangled with other organic matters. As these impurities are more firmly fixed by the calcareous salt than the ferment, the latter can be extracted by water, and subsequently precipitated by alcohol from its watery solution. It is wanting in the pancreas of newly-born infants.

The second pancreatic ferment is known as "trypsine," from its softening effect on coagulated albuminous matters. It acts upon them somewhat like the gastric ferment, transforming them into peptone. The pancreatic juice, as well as the extract of the pancreatic tissue, certainly contains a substance capable of digesting and dissolving coagulated albumen or fibrine; but this action is effected with readiness only in an alkaline or neutral fluid, and is soon followed by putrescence. In an acidulated solution it goes on with difficulty or not at all, and according to Hoppe-Seyler is distinctly interfered with by the presence of hydrochloric acid in the proportion of one part per thousand. It is doubtful how far it takes place during digestion in the fluids of the small intestine, which have normally an acid reaction. Pancreatine and trypsine are accordingly two distinct substances with different properties, the former having an action upon starch, the latter upon albuminous matters. They are also, according to Langendorff,* produced in the embryo at different periods of development; trypsine showing itself at the beginning of the fifth month, while pancreatine only appears after birth.

The third ferment in the pancreatic juice is one which causes the acidification of neutral fats. This change may be produced with either pancreatic juice, infusions of the gland, or fresh moist pieces of the gland tissue, placed in contact, at 38° C., with liquid neutral fat; their normal alkalescence giving place, after a time, to an acidity due to the liberation of fatty acid. So long as any surplus alkali remains, the decomposed fat is saponified; but the proportion which undergoes this additional modification seems to be normally a small one. The pancreatic ferment which causes acidification of the fats has not been obtained in a separate form.

4. Fibrine-ferment.

This is the substance which induces the coagulation of fibrinogen and the production of fibrine in freshly drawn blood. It acts in such minute quantity that its physical and chemical characters have not been accurately determined, and even its source is not fully known. But in some way or other it appears in the blood soon after its discharge from a wounded vessel, or even when its circulation has been arrested by a ligature. It seems to be exuded, perhaps from the interstitial fluids, wherever the walls of the blood-vessels are divided, bruised, degenerated, or inflamed; for at these situations the blood always coagulates. It is obtained, according to the method of Schmidt,† from blood-serum by coagulating it with 15 or 20 times its volume of strong alcohol, and allowing the mixture to remain for two weeks, to secure

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* Archiv für Anatomie und Physiologie. Leipzig, 1879, p. 95.

† Archiv für die gesammte Physiologie. Bonn, 1872, Band VI., p. 413.

complete insolubility of the albuminous matters. The coagulum is then dried, pulverized, treated with water to double the original volume of the serum, and the watery extract filtered. The filtered solution contains the ferment, and if added to a fluid containing fibrinogen will cause its coagulation.

5. Diastase.

Diastase is a vegetable nitrogenous matter, produced in the germination of the cereal grains, and especially of barley, by which their starch is converted into dextrine and sugar. It may be extracted from malting barley with water, the concentrated watery extract being precipitated by alcohol, and the precipitate dried and redissolved in water. Its action is most rapid in a neutral menstruum and at moderately warm temperatures, ceasing about 75° C. It is considered as the representative of the sugar-producing bodies of this group, all those having a similar action being designated as "diastatic" ferments.

MUCIFORM, GELATINOUS, AND SOLID ALBUMENOID SUBSTANCES.

The substances of this group are distinguished rather by their consistency than by their active chemical or physiological properties. They do not form part of the nutritious juices, like albuminous matters, nor give rise to chemical transformations like the ferments. They have reached their final stage in the constructive nutrition of the body, and are useful in facilitating the mechanical movement of the parts, or in holding the other ingredients of the tissues in a coherent mass. They are not easily affected by chemical influences, and most of them show great resistance to the action of ordinary alkaline or acidulated liquids. As a rule, they constitute the organic part of the solid tissues.

1. Mucine.

There are various secretions in the body designated by the common name of "mucus," and distinguished by a peculiar physical character of viscidity and lubricity. This consistency is due to the presence of mucine. It exists in all the varieties of mucus, some of which, like those of the bronchial tubes and intestines, are nearly fluid, while others, like that of the cervix uteri during pregnancy, are gelatinous and semi-solid. It is also present in the synovia, the secretion of the gall-bladder, and the saliva of the submaxillary and sublingual glands. The secretion of the mucous follicles of the mouth consists of it almost exclusively. Like the albuminous matters, it contains carbon, hydrogen, nitrogen, and oxygen, but is destitute of sulphur. In pure water it swells up without becoming liquid, but it is soluble in alkalescent solutions, particularly in those of the alkaline earths, as lime-water and baryta-water. It is not affected by boiling, but is precipitated by acetic acid. It is thought to be held in solution in the mucous secretions by their free alkali; the varying consistency of the secretions being due to the quantity of alkali which they contain. Mucine is unaffected by most of the metallic salts, lead-subacetate being the only one which produces a distinct coagulation. In some cases, as in the bile, it is dissolved in the fluid ingredients of the secretions, from which it may be separated by alcohol. In others, as in the urine, it is only mechanically suspended, subsiding as a light deposit after a few hours' repose.

Mucine is useful mainly by lubricating the opposite surfaces of adjacent organs, as in the synovial cavities; by protecting mucous membranes from the air, as in the trachea and bronchi or by facilitating the mastication and deglutition of food, as in the secretions of the mouth and submaxillary glands.

2. Gelatine.

This substance is very widely diffused in the animal body, forming the more or less homogeneous interstitial mass of the bones, periosteum, tendons, ligaments, fasciæ, and connective tissues generally. All these tissues, although at first insoluble in boiling water, become dissolved after long ebullition; and the dissolved matter solidifies, on cooling, into a jelly-like mass. This substance is the animal principle of glue. It was formerly doubted whether gelatine represents the original ingredient of the fibrous and bony tissues, or an altered product due to continued ebullition. Comparative analyses, however, of the gelatigenous tissues and of the gelatine extracted from them have shown that there is not only no appreciable difference in their chemical constitution, but that the solid residue of the dried tissue and that of the gelatine extracted from it are the same in weight. (Hoppe-Seyler.)

A hot solution of this substance gelatinizes on cooling when present in the proportion of 3 per cent.; below this quantity, or if the boiling be repeated, it may remain liquid. Its solution rotates the plane of polarization to the left 130°. It is thrown down by alcohol and by tannic acid. The last, which is the only acid by which this substance is precipitated, is a very sensitive test of its presence; and, according to Hardy,* will detect one part of gelatine in 5,000 parts of water. A similar combination takes place, in the process of tanning, between tannic acid and the substance of the fibrous tissues, by which they are rendered harder, more impermeable to water, and incapable of putrefaction. Gelatine is not affected by potassium ferrocyanide with acetic acid, nor by lead subacetate. It contains sulphur as one of its ingredients.

3. Chondrine.

The intercellular substance of cartilage resembles that of the bones and the fibrous tissues in yielding, by prolonged boiling with water, a substance which will gelatinize on cooling. In the case of the cartilages, however, this substance is termed *chondrine*, from the source from which it is derived. Chondrine, like gelatine, contains sulphur,

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* Chimie Biologique. Paris, 1871, p. 282.

and presents for the most part similar chemical reactions. It differs from gelatine in being precipitated from its watery solution by both acetic acid and lead subacetate. It rotates the plane of polarization to the left 213.5°.

4. Elastine.

The fibres of all the yellow elastic tissues, as in the middle coat of the larger arteries, the elastic ligaments of the spinal column, and the ligamentum nuchæ, consist mainly of a homogeneous substance distinguished by its refractory nature toward chemical reagents. It is obtained by boiling the elastic tissues successively with alcohol, ether, water, acetic acid, dilute soda solution, and dilute hydrochloric acid. The elastine, thus purified from other ingredients, is not itself soluble in either of the above liquids. It is not converted into gelatine even by long boiling; and it is dissolved, but at the same time decomposed, only by the concentrated acids and alkalies. The slender elastic fibres mingled with connective tissue, and the sarcolemma of the striped muscular fibres, are probably composed of the same substance. Elastine contains no sulphur.

5. Keratine.

This is the exceedingly resisting and indestructible substance of the hair, nails, epidermis, feathers, and all horny tissues. It is unaffected by boiling with alcohol, ether, water, or the dilute acids. By continuous boiling in a Papin's digester at 150° C. it is liquefied and partly decomposed. It is distinguished from the preceding substance by containing sulphur as an ingredient; and when decomposed by boiling under pressure or with concentrated alkalies, it gives rise to hydrogen sulphide vapors.

Source, Changes, and Destination of the Albumenoid Substances.—The source of albumenoid substances in the animal body is in the food. Herbivorous animals take them ready formed in the juices and parenchyma of plants, and the carnivora are supplied with them in still greater quantity in the animal tissues. Man obtains them from both sources, and all nutritious articles of food contain them in greater or less abundance. According to the estimates of Payen, which correspond very closely with our own observations, an adult man requires a daily supply of about 130 grammes of albumenoid matter to provide for the wants of the system; and this quantity is actually contained in the food consumed.

But although albumenoid matter is thus abundantly supplied to the system from without, yet the particular substances characteristic of the various tissues and fluids are formed within the body, by transformation of those introduced with the food. None of the albumenoids contained in the food of an herbivorous animal are precisely identical with those of his own body. All the tissues and juices of the embryo chick are formed from the albumen of the egg; and the nourishment of all the organs of the infant is provided at the expense of caseine, the albumenoid element of milk. There are many different kinds of these substances in the solid parts and secretions of the adult body, but not one of them is contained under its own form in the blood, from which all the nutritious material for the tissues and glands is supplied. It is evident that the albumenoid substances finally present in the animal frame are produced by transformation from those contained in the food and in the blood.

Only a very small proportion of the albumenoid substances is discharged with the excretions. Those contained in the perspiration, the sebaceous matter, and the mucus of the urinary bladder and large intestine are almost the only ones which find an exit in this way. A very little albumenoid matter is exhaled in a volatile form with the breath, and a little also, in all probability, from the skin. But the entire quantity so discharged bears an insignificant proportion to that introduced with the food. The albumenoid substances, accordingly, are decomposed in the interior of the body. After being produced by metamorphosis in the act of nutrition, they are still further transformed in the process of destructive assimilation, and they are represented, in the excreted products, by other combinations of a different form.

CHAPTER V.

COLORING MATTERS.

SOME of the animal tissues and fluids are distinguished, in addition to their other features, by characteristic colors, due to the presence of certain coloring matters. In some instances, as in the red globules of the blood, and the green leaves of plants, the coloring matters are directly connected with active physiological functions. In others, as in the choroid coat of the eye, they are essential to the physical phenomena of the organs to which they belong. But notwithstanding the evident importance of these substances, and the striking character of their optical properties, they are in many respects more difficult of study than the other ingredients of the body. This is partly due to the comparatively small quantity in which they occur, and to the readiness with which they are decomposed or altered in the process of separation; and it is sometimes difficult to decide whether a variation of tint be due to the different proportions of several coloring matters or to the varying degrees of concentration of a single one.

The coloring matters are all nitrogenous compounds, but differ in essential particulars from the albumenoid substances. Those which have been most fully examined are known to be crystallizable; and it is probable that all of them might be obtained in a crystalline form, could they be completely separated without decomposition. The most remarkable of all, and that which possesses the most important physiological properties in the animal body, is the red coloring matter of the blood. It appears to be analogous in many respects to the green matter of leaves and leaflike organs in the vegetable world. Each of these two coloring matters is the most abundant and widely diffused in its own kingdom, and is distinguished by the identity of its characters in many different species of animals and plants respectively. While the red coloring matter of the blood, on the one hand, is the agent by which oxygen is absorbed and distributed in the animal body; on the other, it is the green coloring matter of plants by which carbonic acid and water are decomposed and oxygen set free in the act of vegetation. It is believed by many that all the coloring matters of the body, in man and the vertebrate animals, are derived by transformation from the coloring matter of the blood; and although we have no complete proof that this is true in all cases, yet it is evident that these substances have a close physiological relation with each other, perhaps as distinct and real as that between the various members of the albuminous or saccharine groups.

The organic coloring matters may be conveniently removed from liquids containing them by the action of *animal charcoal;* that is, carbon derived from the imperfect combustion of animal substances. If a fluid containing either of the coloring matters be mixed with a sufficient quantity of this charcoal and filtered, the filtered fluid will pass through colorless. Albuminous substances are also retained upon the filter when treated with animal charcoal; while glucose and other crystallizable and saline matters pass through freely in solution.

The animal coloring matters most distinctly recognized are those of the blood, the blackish-brown tissues, the bile, and the urine.

1. Hemoglobine, $C_{600}H_{960}N_{154}FeS_3O_{179}$.

This is the coloring matter of the red globules of the blood, the most abundant and important substance belonging to this group. It forms much the largest proportion of the solid ingredients of the dried blood-globules, and amounts to from 25 to 30 per cent. of their weight in the fresh condition. It is also found, in much smaller quantity, in the substance of the muscular tissue, of which it forms the coloring principle. It crystallizes in well marked forms, which vary somewhat in different species of animals; but are all, so far as known, either rhombic or hexagonal tables or prisms. It is soluble in water, in very dilute alcohol, and in dilute solutions of albumen, of the alkalies, and their carbonates, and of sodium and ammonium phosphates. It is insoluble in strong alcohol, in ether, and in the volatile and fatty oils. In almost every condition it is readily decomposed. According to Preyer,* crystals which have been thoroughly dried at a temperature below the freezing-point become, after a time, decomposed, and lose their color and solubility, even at ordinary temperatures. A watery solution of hemoglobine kept at any temperature above the freezing-point of water becomes altered in the course of twenty-four hours, and if heated to 64° C. it is at once decomposed.

Fig. 12.

Hemoglobine Crystals; from human blood. (Funke.)

Hemoglobine, when crystallized, presents the bright red color of arterial blood. It is distinguished beyond all other known ingredients

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* Die Blutkrystalle. Jena, 1871, p. 58.

of the body, by its capacity for absorbing oxygen, which it retains in the form of a loose combination. According to the average result of various experiments one gramme of hemoglobine, in watery solution, will absorb 1.27 cubic centimetres of oxygen. It is again deprived of its superabundant oxygen under the influence of diminished pressure, heat, or the continued displacing action of hydrogen or nitrogen. Its hue varies according to these two conditions, being bright red in the former case, dark red or purple in the latter. It is therefore known under two different forms; namely, that of "oxyhemoglobine," containing its full quota of loosely combined oxygen, and that of "reduced hemoglobine," in which the surplus oxygen has been removed. Its presence, in either one or the other of these conditions, is the cause of the color of arterial and venous blood.

Spectrum of Hemoglobine.—All transparent coloring matters, when viewed by transmitted light, absorb or arrest certain portions of the luminous ray and allow others to pass. The transmitted beam, therefore, appears colored, because only a part of the original white light reaches the eye. If, after passing through a colored solution, the luminous ray be analyzed into its spectrum by means of a prism, as in the spectroscope, it can then be seen exactly what colors have been allowed to pass the solution, and what have been retained by absorption. Wherever a color has been absorbed or arrested, its place in the spectrum is occupied by a dark band. Such a band occurring in the spectrum of any colored substance, is called an "absorption band," and becomes a distinguishing feature in the spectrum of that substance.

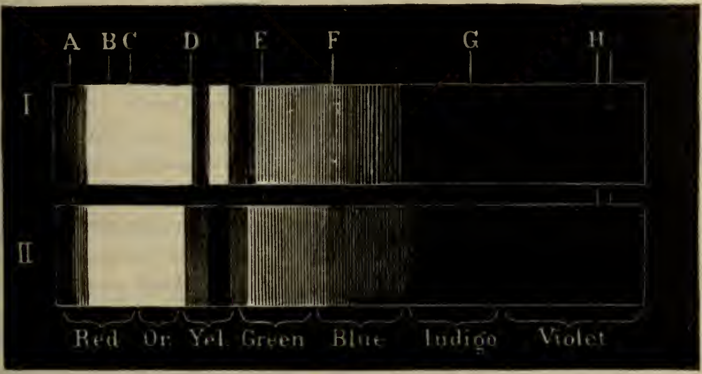
The spectrum of hemoglobine, in an aerated solution, is distinguished by two separate absorption bands. The first is a comparatively narrow, dark, and well-defined band situated in the yellow, a little to the right of the line D. The second is a wider, fainter, and more diffused band, at the commencement of the green, and a short distance to the left of the line E. Both bands are, therefore, contained in the space between the lines D and E. Beyond E the green and blue of the spectrum are visible, but the light diminishes gradually and disappears near the end of the blue, so that the indigo and violet parts are completely dark. Fresh blood, diluted with water, will give the same appearance.

If the solution be concentrated, or viewed in a very thick layer, it is too opaque for spectroscopic examination, and may shut off all the light of the spectrum except a little of the red and orange; if too dilute, it will fail to exhibit its distinguishing characters. A solution of a certain strength, which allows abundance of light to pass, and is yet sufficient to cause its absorption at particular points, is best suited for examination. With pure hemoglobine, according to Preyer, a solution of about 1.5 parts per thousand gives the most marked results. With fresh blood, if one volume of the defibrinated blood be diluted with one hundred volumes of water, and the mixture viewed in a layer of one centimetre, all the characteristic traits of the spectrum will be distinctly shown. (Fig. 13, I.)

These characters form a very delicate test for the coloring matter of blood. Preyer has found that with a solution of pure hemoglobine in water, of 4 parts per ten thousand, the absorption bands may still be seen, though the second one is very faint; and according to Hoppe-Seyler, a solution of one part in ten thousand will allow them to be recognized if viewed in a layer one centimetre in thickness. Fresh dog's blood, if diluted with 1,000 parts of water, and viewed in a layer of 3 centimetres' thickness, will show a spectrum in which both absorption bands are distinctly perceptible though not very strong. If diluted with 10,000 parts of water, and viewed in a layer of 4.5 centimetres, the first band is still visible, though very faint; the second is imperceptible.

The condition of hemoglobine, in regard to its absorption of oxygen, has a marked effect on its spectroscopic characters. The spectrum with two absorption bands, above described, is that of hemoglobine which has absorbed all the oxygen which it is capable of holding in loose combination. If this oxygen be removed, the color of the solution is modified and its spectrum changes. The coloring matter is no longer oxyhemoglobine, but has become reduced hemoglobine; and its spectrum, instead of two absorption bands, shows but one, comparatively wide and ill-defined, the darkest part of which occupies exactly the space formerly intervening between the two. At the same time the dim borders of the obscured portion shift toward the left; so that the orange in the neighborhood of the line D is less brilliant than before, while nearly the whole of the green becomes visible to the left of the line E. The blue is also extended a little toward the right. (Fig. 13, II.)

FIG. 13.



I. Spectrum of Oxyhemoglobine.
II. Spectrum of Reduced Hemoglobine.

The coloring matter of the blood may be deprived of its loosely combined oxygen by evacuation with the air-pump, treatment with a current of hydrogen or nitrogen, the addition of deoxidizing agents, or by keeping the blood or its solutions protected from the access of air. The last method is most easily applied. If a solution of fresh blood, of a bright scarlet color, which yields a spectrum with the absorption bands of oxyhemoglobine fully developed, be inclosed in a securely stopped test-tube, the whole of which it completely fills, and kept in this condition for twenty-four or forty-eight hours, the hemoglobine at the end of that time will have lost its surplus oxygen, and if placed before the spectroscope, the solution will show a spectrum with the single absorption band of reduced hemoglobine. If the test-tube be now opened, the solution transferred to a larger vessel, and shaken up for a few seconds with atmospheric air, its bright color returns, the single absorption band disappears from its spectrum, and the two absorption bands of oxyhemoglobine again become visible.

The spectroscopic characters of hemoglobine are of value in showing that this substance, as extracted in the crystalline form, is identical with the normal coloring matter of the fresh globules. A solution of crystallized hemoglobine gives the same spectrum with solutions of fresh blood or with the dried globules. The blood, while still circulating in the vessels, may also be made to exhibit the same appearances. If a spectroscope eye-piece with two prisms be attached to the body of a microscope in such a way that two spectra may be seen in the field, one above another, one formed by the light coming through the body of the instrument, the other by that coming through a lateral opening in the eye-piece; and if the mesentery of a living frog be placed before the objective of the microscope, while a solution of human blood is placed at the lateral opening, it will be seen that the absorption bands in the two spectra correspond exactly with each other.

The hemoglobine from different animals varies somewhat in the form of its crystals, in their degree of solubility in water, and, according to several analyses, in the exact percentage of its constituent elements. But its spectroscopic characters are remarkably invariable; and their immediate connection with its essential physiological property, namely, the absorption and discharge of oxygen, shows them to be the most important marks for its identification. By this means the existence of hemoglobine in the blood-globules has been demonstrated in such different animals as the dog, fox, cat, horse, sheep, pig, lion, cougar, baboon, bat, hedge-hog, rat, guinea-pig, squirrel, mole, goose, pigeon, lark, owl, crow, lizard, python, tortoise, frog, carp, perch, herring, and pike. It has been discovered, in all, in 22 species of mammalians, 7 birds, 5 reptiles, and 12 fish; and exists in every species of vertebrate animal which has been examined for that purpose. Even in several invertebrate species, where the blood is of a red color, although exhibiting no distinct globules, it is found to contain hemoglobine in a state of solution. Preyer found that the red circulating fluid of the earthworm, when examined by the spectroscope, yields a spectrum with two absorption bands identical with those of human hemoglobine. It has also been discovered in the blood of the pond-snail, the horse-leech, and the fresh-water shrimp.

Functional Activity and Changes of Hemoglobine in the Body.—Hemoglobine is the most active of all the coloring matters in the animal system. It absorbs oxygen from the air in the lungs, and thus provides an incessant supply for the whole body. But this absorption is not a process of oxidation. The oxyhemoglobine holds its oxygen in loose combination, and readily parts with it in the general circulation, returning to the state of reduced hemoglobine in the venous blood. Each of these two properties is equally important with the other, for it is by this means that the oxygen of the lungs finds its way into the system at large.

A marked feature in the chemical constitution of hemoglobine is that it contains iron. This fact is the more important because it is the only substance in the animal body, excepting hair, which contains iron in any considerable amount, and because iron is also requisite for the formation of the green coloring matter of plants. Experiment has shown that without iron vegetation cannot go on; and there is reason to believe that it is equally essential to the constitution of the animal coloring matter, and thus indirectly to the general nutrition of the animal body. It is present in hemoglobine, in all probability, not in the form of a distinct oxide, but directly combined, like sulphur, with the carbon, hydrogen, nitrogen, and oxygen which form the remainder of its substance.

One thousand parts of hemoglobine contain 4.2 parts of iron; and, according to the average results obtained by different observers, healthy human blood contains, per thousand parts, 123.4 parts of hemoglobine, and 0.52 parts of iron. The human body, according to the lowest authentic estimate, contains 8 per cent. of its weight of blood, which would give, for a man weighing 65 kilogrammes, 2.71 grammes of iron in the blood of the whole body.

The iron of the hemoglobine passes out by the bile and the urine, both of which contain traces of its presence. It is also contained in the hair, where it forms nearly 7 per cent. of the incombustible ingredients. It is supplied to the body by ordinary food, in which it is always present in appreciable amount. Since hemoglobine exists to some extent in the muscular tissue, it will be present in a more or less altered form, but still containing iron, in most kinds of animal food. According to the analyses of Moleschott, 500 grammes of beef (about one pound avoirdupois) will contain 0.035 gramme of iron; and it is found in even larger proportion in rye, barley, oats, wheat, peas, and especially in strawberries. As the quantity of this substance discharged daily in the urine and the bile is so small, we must regard the greater portion of that which passes through the system as used in the growth of the hair; and a very moderate amount in the food is sufficient for the requirements of nutrition.

2. Melanine.

In all the dark-colored tissues of the body, in the choroid coat of the eye, the rete Malpighi of the skin in the black and brown races, and in individuals of dark complexion, in the hair, and in the substance of melanotic tumors, there exists a coloring matter known as melanine. When isolated or collected in compact masses, it is of a very dark blackish-brown color; but by its mixture, in different proportions, with other colorless or ruddy semi-transparent ingredients of the tissues, it may produce all the varying grades of hue, from light yellowish-brown to nearly absolute black. It is deposited in the substance of cells in the form of minute granules, and is usually more abundant in the immediate neighborhood of the nucleus than near the edges of the cell. A substance regarded as melanine has also been found by several observers in certain morbid deposits under the crystalline form, especially as flat rhombic tablets with acute angles.

The elementary analyses of melanine derived from different sources do not exactly correspond with each other, although they approximate within moderate limits. As the average result of analyses collected by Hoppe-Seyler,* it contains, freed from ashes, the following proportions, by weight, of carbon, hydrogen, nitrogen, and oxygen.

Composition of Melanine.

Carbon	54.39
Hydrogen	5.08
Nitrogen	11.17
Oxygen	29.36
	100.00

Repeated observations show that it also contains iron, which has been found by Lehmann in the proportion of 2.5 parts per thousand.

Melanine is insoluble in water, alcohol, ether, and solutions of the organic and mineral acids. Boiling solutions of potassium hydrate dissolve it without change of color, but its color is destroyed by chlorine.

Melanine is supposed to be produced by metamorphosis from the hemoglobine of the blood. The fact that it contains iron gives a certain probability to this view; and it is a repeated observation that black or blackish staining of the tissues sometimes appears in and around old spots of congestion or ecchymosis. It also forms the principal coloring matter of the hair, which probably contains most of the iron derived from destructive assimilation of the blood-globules.

3. Bilirubine, $C_{16}H_{18}N_2O_3$.

The red or orange-red coloring matter of the bile. This substance has been designated, by different writers, under the various names of Biliphæin, Bilifulvine, Hematoidine, and Cholepyrrhine. It is formed

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* Handbuch der Physiologisch und Pathologisch-Chemischen Analyse. Berlin, 1870, p. 177.

in the liver, and may be extracted from its tissue in a pure form. From the liver cells it is taken up by the biliary ducts and mingled with the other ingredients of the bile. It is crystallizable, soluble in chloroform, less so in alcohol, and slightly soluble in ether. It is readily soluble in alkaline liquids, but quite insoluble in pure water. In the crystallized form it is red; in the amorphous condition, orange; and in solution, reddish-brown or yellow, according to the degree of concentration. According to Hoppe-Seyler, it gives a perceptible yellow color when viewed in a layer 1.5 centimetre in thickness, even if dissolved in 500,000 times its weight of fluid.

Solutions of bilirubine exhibit a well-marked reaction with nitroso-nitric acid, known as "Gmelin's bile test." If such a solution be treated with a small quantity of nitric acid, tinged with nitrous acid, a series of colors is presented in the following order: green, blue, violet, red, and finally a dingy yellow. These colors are produced by transformation of the bilirubine, and represent successive degrees of its oxidation. The reaction is a very sensitive one, and, according to Hoppe-Seyler, will produce a visible result in solutions containing only one part in 70,000.

Bilirubine is generally regarded as derived from hemoglobine. The reasons for this opinion are: First, its reddish color, somewhat similar to that of diluted blood. Secondly, it has been found in various parts of the body, in old bloody extravasations, evidently produced from an alteration of the blood upon the spot. When found under these circumstances, it was formerly known as *hematoidine.* Thirdly, if the blood-globules be made to assume a liquid form by alternately freezing and thawing a portion of freshly drawn blood, and this blood then re-injected into the blood-vessels, the operation is followed by a discharge of bilirubine in the urine. If hemoglobine be, in fact, normally transformed into bilirubine, its iron and sulphur must enter into some other combination, as neither of these elements exists in the coloring matter of the bile. Bilirubine, if exposed to the air in alkaline solution, becomes oxidized and assumes a green color, being converted into the following closely related substance, biliverdine.

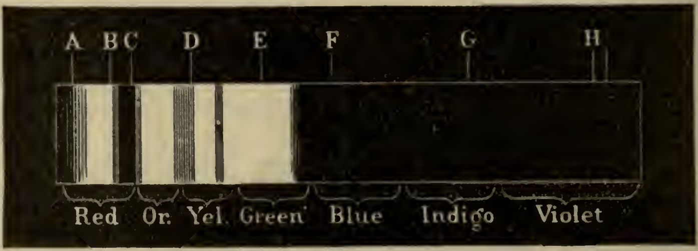
4. Biliverdine, $C_{16}H_{20}N_2O_5$.

In addition to bilirubine, the bile contains a green substance, known as biliverdine; and the varying tint of different specimens of bile depends on the proportion in which the two coloring matters are present. In man and the carnivorous and omnivorous animals, the bile is bronze, brown, yellowish, or orange, owing to the presence of bilirubine; while in the ox, sheep, rabbit, and vegetable feeders generally, it presents a strong green or greenish color, due to the comparative abundance of biliverdine. Biliverdine is insoluble in water, ether, and chloroform, readily soluble in dilute alkaline solutions and in alcohol. It is also soluble in glacial acetic acid, and is deposited from the evaporated solution in a form of imperfect crystallization. It is often found in human gall stones, and in the dog is abundantly deposited along the edges of the placenta.

The *spectrum* of biliverdine is marked by a very distinct and dark absorption band in the red, at the situation of the line C, extending thence to the left toward the line B. Its width increases with the thickness of the layer of fluid examined, and when this exceeds a certain limit the whole of the red disappears. The band rarely reaches the situation of the line B, and seldom or never passes beyond it, without extinguishing at the same time all the red light of the spectrum. In layers of green bile, two or three centimetres in thickness, it is quite dark, often almost black, while the red on each side of it is still very brilliant.

As a rule, the intensity of the absorption band at C is in proportion to the preponderance of green in the color of the bile. Though easily seen, in comparatively thin layers, in specimens of a pure green or a decided greenish-olive color, it is less perceptible in those of a yellowish, yellowish-brown, or olive-brown tint. But if a specimen of reddish or yellowish-brown bile, which does not show the band distinctly, be turned green by the addition of a few drops of an iodine solution, the band at C at once becomes visible, often to a very marked degree. It is, therefore, no doubt the characteristic absorption band of biliverdine. (Fig. 14.)

Fig. 14.



Spectrum of Green (Sheep's) Bile.

There are two other absorption bands in the spectrum of bile, less constant and much less distinct than that at the line C. One of them, very dim and ill-defined, is situated at the junction of the orange and yellow, immediately to the left of the line D, occupying about the last third of the space between C and D. The remaining band is much narrower than either of the others, but somewhat more distinct than the second. It is situated in the yellow, at about one-third the distance between D and E. The last two bands are more frequently visible in sheep's bile than in that of other animals; but all three may be sometimes seen in a watery solution of desiccated ox-bile, which has been kept, in the form of a dry powder, for several years.

The spectrum of bile also exhibits a remarkable diminution in intensity of the orange and yellow colors. The situation of the second absorption band, at the junction of these colors, will account for a part of this diminution; but the spectrum is also very dim in the space between the second and third absorption bands, where the normal spectrum of solar light is brightest. This is the place naturally occupied by yellow, but in the great majority of cases, in the spectrum of bile, there is no pure yellow perceptible, and but little or no orange. The situation of these two colors is encroached upon by the red and green respectively; and in not a few instances, as the spectrum terminates before the commencement of the blue, the only colors really perceptible in it are red and green. The line C in the normal spectrum is situated at the junction of the red and orange, and yet the principal absorption band at this point, when viewed in the spectrum of bile, appears to be situated entirely in the red, owing to this color taking the place of the orange on the right of the line C. This peculiarity shows itself in the spectrum of bile, whether the color of the specimen be greenish or yellowish-brown.

There is another spectroscopic feature in bile, due to its containing more or less of two different coloring matters.

If a tolerably thick layer of bile be placed before the spectroscope, and the slit of the instrument gradually opened, the first light which appears in the spectrum is usually a *green* light, in the latter half of the space between D and E. On continuing to increase the size of the opening, if the bile be deeply colored, the next to appear is a *red* light, at the extreme end of the spectrum between A and B; in less concentrated specimens the red light may show itself simultaneously on both sides of the absorption band at C. Afterward the green light extends further toward the left until the spectrum is complete. The order in which these appearances follow each other depends upon the relative quantity of bilirubine or biliverdine.

There is reason to believe that biliverdine is formed from bilirubine by a process of hydration and oxidation, the elements of water entering at the same time into combination. The nature of this change is shown by the following formula:

$$\underset{\text{Bilirubine.}}{C_{16}H_{18}N_2O_3} + H_2O + O = \underset{\text{Biliverdine.}}{C_{16}H_{20}N_2O_5}.$$

The prompt conversion of the color of ruddy or reddish-brown bile into green by the action of various oxidizing agents, or even by exposure to the air, and the evident chemical relationship between the two substances, leave no doubt that this is the origin of biliverdine. Both bilirubine and biliverdine are discharged with the bile into the alimentary canal, where they become undistinguishable toward the lower end of the small intestine. Beyond that point they are replaced by the brown coloring matter of the feces, and are finally discharged from the body under this form.

5. Urochrome.

The coloring matter of the urine has been repeatedly studied, but thus far with only partial success. The substances which have been extracted from the urine by various methods, as representing, more or less exactly, its natural coloring matter, are known by the names of Urochrome, Urosine, Urosacine, Hemaphæine, Urohematine, Uroxanthine, Urobiline, and Hydrobilirubine. Most of them are probably modifications of the same substance, variously altered by the methods of extraction, or obtained in different grades of purity. The fresh, normal urine has a light yellowish or amber color, while specimens of unusually high specific gravity, and particularly specimens of febrile urine, often exhibit a distinct reddish hue. Normal urine, which, when fresh, is only amber-colored, will often acquire, by exposure to the air, a tinge of red. The substance obtained by Thudichum,[*] and called by him urochrome, is precipitable from the urine by various metallic salts. It has not yet been produced in a crystalline form. It is soluble in water and in ether, but only slightly soluble in alcohol. Its watery solution has a yellowish color, which, on standing, becomes red. *Urohematine* (Harley) is nitrogenous in composition, and contains iron.[†] It is insoluble in pure water, but soluble in the fresh urine, as well as in ether, chloroform, and alcohol. The substance termed *Urobiline* (Jaffé) was so named to indicate its derivation from the coloring matter of the bile. It is identical with *hydrobilirubine* (Maly), which is produced from bilirubine by hydration and deoxidation by means of sodium-amalgam. The change which takes place in this process is as follows:

$$\underset{\text{Bilirubine.}}{2(C_{16}H_{18}N_2O_3)} + 2(H_2O) - O = \underset{\text{Urobiline.}}{C_{32}H_{40}N_4O_7}.$$

Urobiline is soluble in alcohol, ether, and chloroform. Its solutions have a brownish-yellow color, and, by dilution, become first yellow, and lastly faint rosy-red. It was found by Jaffé[‡] in many cases in human urine, where it was recognized, after partial extraction and purification, by its spectroscopic properties; showing an absorption band at the junction of the green and the blue, between the lines E and F. But the same observer found that fresh urine, not subjected to chemical manipulation, would often present no indication of urobiline. If secluded from the atmosphere, it would remain light-colored; but if exposed to the air from two to twelve hours, it would become darker in hue, and at the same time would show, by the spectroscope, signs of urobiline. This substance consequently is not now regarded as the normal coloring matter of the urine, but as a product of its alteration.

It is evident, however, that the urine contains a coloring matter, derived in all probability from the bile, which gives to it its well-known amber tint. This substance is liable to be changed under the influence of oxidation, and to assume in that condition a more or less distinctly

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[*] British Medical Journal. London, Nov. 5, 1864.

[†] Harley, The Urine and its Derangements. Philadelphia, 1872, p. 97.

[‡] Archiv für pathologische Anatomie und Physiologie, 1869, Band xlvii., p. 405.

red color. Such a modification certainly takes place outside the body, and it may also occur within the system, giving rise to the varying proportions of red in the color of the urine under different healthy and diseased conditions.

6. Chlorophylle.

This is the green coloring matter of plants. It is more widely diffused than any other coloring matter in the vegetable world, and it apparently constitutes the coloring principle of all the green parts of the higher plants without exception. It has been obtained by Gautier* in the crystalline form, as flattened, isolated, or radiating needles, of a softish consistency and an intensely green color; afterward, by exposure to light, they become yellowish-green, then brownish-green, and are lastly decolorized. Its composition is as follows:

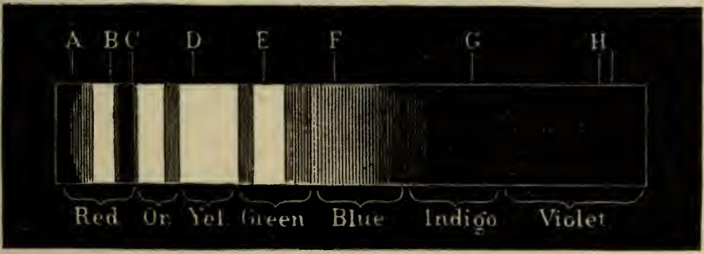
Composition of Chlorophylle.

Carbon	73.97
Hydrogen	9.80
Nitrogen	4.15
Oxygen	10.33
Ash	1.75
	100.00

Its incombustible residue consists mainly of alkaline phosphates. It is completely destitute of iron.

The similarity of chlorophylle to biliverdine, fully recognized by Gautier in regard to some of its chemical reactions, is very strongly marked in its spectroscopic characters. The principal absorption band in the spectra of these two substances is identical in position and appearance. It is the dark band situated in the red, extending from the line C toward B. (Fig. 15.) In an alcoholic solution of chlorophylle, extracted from green grass or leaves, there are three additional bands, less prominent than the former, and differing from those of bile. One of these additional bands is placed at the edge of

Fig. 15.



Spectrum of Chlorophylle in Alcoholic Solution.

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* Comptes Rendus de l' Académie des Sciences. Paris, 1879. Tom. lxxxix., p. 861.

the orange, between C and D; another at the beginning of the green, on the left of E; and a third, wider than the others, but very faint and ill-defined, at the termination of the green, between E and F. In the spectrum of chlorophylle, the yellow of the spectrum appears in its proper place and with nearly its natural hue. The light, also, extends beyond the green, throughout the blue, and a little into the commencement of the indigo.

Chlorophylle is of the first importance in vegetable physiology, as it is under the influence of this substance, and that of the solar light, that the inorganic ingredients of the soil and the atmosphere are deoxidized and combined to form a carbo-hydrate. The process of vegetation proper, that is, the production and accumulation of organic material in the form of starch, sugar, cellulose, and the substance of various vegetable tissues, is inseparably dependent on the action of chlorophylle. But to produce this effect, the chlorophylle must constitute a part of the living vegetable cell. The coloring matter alone, extracted from the chlorophylle-holding cells, and placed under all other conditions, such as air, sunlight, warmth, and moisture, known to be essential to the work of production, is incapable of forming organic matter out of water and carbonic acid. Its function is not that of a simple chemical reagent, but that of an active constituent of the living organism.

Chlorophylle is produced, in the interior of the vegetable cell, sometimes as a uniformly diffused mass. Usually, however, it is deposited in rounded grains, frequently arranged in definite figures or patterns within the cell. It may be extracted by alcohol or ether, and retains its green color when in solution in these substances. It disappears previously to the shedding of the leaves, when they cease the act of vegetation, and is usually replaced by grains of a red or yellowish color.

CHAPTER VI.

CRYSTALLIZABLE NITROGENOUS MATTERS.

THE fifth and last group of bodily ingredients consists of a number of colorless substances, which resemble the albumenoids in containing nitrogen, but differ from them in being crystallizable. Many of them are evidently derived from the albumenoids by retrograde metamorphosis, being discharged from the system as products of excretion. Others do not exhibit this character, and are found only in the permanent tissues or the internal fluids. Several of them, though undoubtedly of importance in the constitution of the body, are still obscure in their physiological relations.

1. Lecithine, $C_{44}H_{90}NPO_9$,

From Λέκιϑος, the yolk of egg, in which substance it was first discovered. Lecithine was formerly described under the name of *phosphorized fat*, owing to the circumstance that one of the products of its decomposition is phosphoglyceric acid ($C_3H_9PO_6$). It is not, however, a fatty substance, since it contains nitrogen, and otherwise differs from the fats. As mingled or combined with other animal matters, it has also been known by the name of "protagon." Lecithine is of very wide distribution in both the animal and vegetable kingdoms, occurring in the cereal grains and leguminous seeds, and, according to Hoppe-Seyler, in the cellular juices of a variety of plants. It is found in the blood, both in the plasma and the globules, in the bile, the spermatic fluid, the yolk of egg, and particularly in the brain, spinal cord, and nerves. In the plasma of the blood, it is in the proportion of 0.4 part per thousand, and in the fresh substance of the calf's brain, according to the analyses of Petrowsky,* in the proportion of 31 parts per thousand. Taking into account the watery ingredients of the brain, lecithine is about equally abundant in the white and gray substance; but of the solid matters alone, it constitutes a little less than 10 per cent. in the white substance, and rather more than 17 per cent. in the gray substance.

Lecithine obtained from either of these sources is an indistinctly crystallizable substance, of waxy consistency, liquefying at a gentle heat, readily soluble in alcohol, less so in ether, and to some extent in chloroform and the fatty oils. If treated with water, it swells into a pasty mass without dissolving, and gives origin, under the microscope, to the appearances known as "myeline forms;" that is, a great

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* Archiv für die gesammte Physiologie. Bonn, 1873, Band vii., p. 101.

variety of mucilaginous or oily looking drops and filaments, of double contour, which exude from the edges of the mass, and remain separate and insoluble; resembling the microscopic forms produced under similar circumstances from the "myeline," or medullary layer of nerve fibres. It is readily decomposed on standing, either in solution or in a state of watery imbibition, acquiring an acid reaction. Decomposition is also effected by acids or alkalies. By boiling with baryta-water it suffers a characteristic alteration, giving rise to the production of two new bodies; namely, a nitrogenous alkaline substance and phosphoglyceric acid.

As to the physiological character or significance of lecithine we are entirely in the dark, except in one respect. It is the only organic combination in the body containing phosphorus. Considering the many articles of food in which it is an ingredient, it must be introduced, in no small quantity, with the nutriment; and it certainly exists abundantly in the substance of the nerves and nervous centres. But as no known organic combination of phosphorus is discharged with the excretions, this substance must pass out of the body as part of the phosphates in the urine and the perspiration. On this account, together with the fact of the constant consumption of oxygen by the animal body, it is believed that the phosphorus, introduced as an ingredient of organic materials, is converted in the system into phosphoric acid, and appears finally under the form of phosphatic salts.

2. Cerebrine, $C_{17}H_{33}NO_3$.

As its name indicates, this is an ingredient of the brain and nerves, the only parts of the body in which it is known to exist. Although not yet obtained in a crystalline form, it is placed among the members of this group because it resembles them in its general features of chemical composition, particularly in its small proportion of nitrogen, and also in certain reactions, which are entirely dissimilar to those of an albuminous matter.

Cerebrine is insoluble in water, but if treated with boiling water it swells, softens, and yields an emulsion. It is insoluble in cold alcohol and ether, but soluble in boiling alcohol and ether, from which it is again deposited on cooling. Boiling with baryta-water decomposes it slowly and incompletely, and does not produce phosphoglyceric acid, as cerebrine contains no phosphorus. If strongly heated in the air, it turns brown, melts, and finally burns with a bright flame.

It is much more abundant in the white than in the gray substance of the brain, forming, according to Petrowsky, in the solid ingredients of the white substance 9.5 per cent., in those of the gray substance but little more than 0.5 per cent. It is undoubtedly a constituent of the medullary layer of nerve fibres, but nothing is known of its origin, metamorphoses, or physiological activity.

3. Leucine, $C_6H_{13}NO_2$.

So called from the glistening snow-white color of its crystals, which are in the form either of thin scaly plates or of radiating needles. It is soluble in water, less so in alcohol, and insoluble in ether. Heated slowly to 170° C., it volatilizes unchanged. At higher temperatures it is decomposed, giving rise, among other products, to carbonic acid and water. Leucine has been extracted from the pancreas and the pancreatic juice, the spleen, thymus, thyroid, lymphatic, parotid, and submaxillary glands, the liver, kidneys, and supra-renal capsules. The pancreas and pancreatic juice are the only situations in which it has been found in abundance; elsewhere it is in very small quantity, though its exact proportions have not been determined. It does not occur in the blood in a state of health, and has been found in the urine only in certain cases of disease.

It appears as one of the results of the artificial decomposition of albuminous matters, by the action of acids or alkalies, and also in the ordinary putrefaction of these substances. It is often found among the products of artificial digestion of albumenoid substances by the trypsine ferment of the pancreas and pancreatic juice; but it is doubtful whether any importance should be attributed to it in this respect, since its quantity in the intestine, during normal digestion, is found by Schmidt-Mulheim* to be quite insignificant.

Physiologists generally agree in considering leucine, in the living body, as derived from albumenoid substances in the act of retrogressive metamorphosis. It has never been obtained artificially from any other source than albumenoid matters; and its ready production from these substances, as well as the analogies of its chemical composition, leave hardly a doubt on this point. But as it does not appear normally, either in the blood or in the urine, it must be regarded only as a stage of transition, through which the nitrogenous matters pass before being finally converted into the products of excretion.

4. Tyrosine, $C_9H_{11}NO_3$.

This substance occurs in the body only in company with leucine, usually in much smaller quantity; and it also appears with leucine in the products of artificial decomposition, digestion, and putrefaction of albumenoid matters. It was so named from having been early found as an ingredient in old cheese (τυρὸς). When pure it is in the form of acicular crystals, nearly insoluble in cold water, readily soluble in boiling water, insoluble in alcohol and ether. It is regarded as similar to leucine in its physiological relations, and as forming, like that substance, an intermediate step in the destructive assimilation of albumenoid matters.

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* Archiv für Anatomie und Physiologie. Leipzig, 1879, p. 39.

5. Sodium Glycocholate, $C_{26}H_{42}NO_6Na$.

This and the following substance are the characteristic ingredients of the bile. Like the two coloring matters of this secretion, they are mingled in various proportions, either the one or the other preponderating in different specimens, or in the bile of different animals. Together they are designated as the "biliary salts."

Sodium glycocholate is a saline body, consisting of a nitrogenous organic acid, glycocholic acid ($C_{26}H_{43}NO_6$) in combination with sodium. Glycocholic acid is so called because by boiling with potassium hydrate or baryta-water, or by continued boiling with dilute hydrochloric or sulphuric acids, it is decomposed with the production of two new bodies, namely, *glycine* ($C_2H_5NO_2$), a nitrogenous neutral substance, and *cholic acid* ($C_{24}H_{40}O_5$), a non-nitrogenous organic acid, so called because peculiar to the bile. This change takes place with the assumption of the elements of water, as follows:

$$\underset{\text{Glycocholic acid.}}{C_{26}H_{43}NO_6} + H_2O = \underset{\text{Glycine.}}{C_2H_5NO_2} + \underset{\text{Cholic acid.}}{C_{24}H_{40}O_5}.$$

Sodium glycocholate is a neutral crystallizable substance, very soluble in water and in alcohol, insoluble in ether. It is extracted from the bile as follows: The bile is evaporated to dryness over the water-bath, the dry residue extracted with absolute alcohol, the alcoholic solution decolorized with animal charcoal, and then mixed with from 8 to 10 times its volume of ether. A whitish precipitate is thrown down, which collects in drops and masses, of a consistency like that of Canada balsam, whence the biliary salts are sometimes termed the "resinous" matters of the bile. In the course of 24 hours, sometimes only after four or five days, the sodium glycocholate crystallizes in hemispherical or star-shaped masses of fine radiating needles. The crystals may be preserved indefinitely in the mixture of alcohol and ether; but if the liquid be poured off, the cold produced by evaporation causes a condensation of atmospheric moisture and a rapid solution of the crystals, which liquefy into transparent, rounded, oleaginous-looking drops. The solubility of these drops in water and their insolubility in ether will distinguish them from oil globules, which they closely resemble in their optical properties. Sodium glycocholate may be precipitated from its watery solution by both the

FIG. 16.

SODIUM GLYCOCHOLATE FROM OX-BILE, after two days' crystallization. At the lower part of the figure the crystals are melting into drops, from evaporation of the ether and absorption of moisture.

neutral and tribasic lead acetates. Its alcoholic solution rotates the plane of polarization toward the right 25.7°.

6. Sodium Taurocholate, $C_{26}H_{44}NSO_7Na$.

This substance, the second characteristic ingredient of the bile, is similar in many respects to the foregoing. Its organic acid, taurocholic acid ($C_{26}H_{45}NSO_7$), is distinguished by containing an atom of sulphur, owing perhaps to its derivation from albuminous matters. If so, glycocholic acid must represent a product of further alteration, in which sulphur, hydrogen, and oxygen are given up in such proportions that the products of elimination are water and sulphur, as follows:

$$\underset{\text{Taurocholic acid.}}{C_{26}H_{45}NSO_7} - H_2O - S = \underset{\text{Glycocholic acid.}}{C_{26}H_{43}NO_6}.$$

By boiling with dilute acids or alkalies, or even with water, as well as under the influence of putrefaction, taurocholic acid is decomposed with the formation of two other bodies, namely, *taurine* ($C_2H_7NSO_3$), a neutral nitrogenous substance, containing the sulphur, so called because first discovered in bullock's bile, and *cholic acid* ($C_{24}H_{40}O_5$), the same body produced by a similar process from glycocholic acid. The change takes place with the assumption of the elements of water, as follows:

$$\underset{\text{Taurocholic acid.}}{C_{26}H_{45}NSO_7} + H_2O = \underset{\text{Taurine.}}{C_2H_7NSO_3} + \underset{\text{Cholic acid.}}{C_{24}H_{40}O_5}.$$

Sodium taurocholate, like the preceding salt, is soluble in water and in alcohol, and insoluble in ether. It is extracted from the bile by a process similar to that already described, and, after precipitation by ether, crystallizes in slender needles, much like those of the glycocholate. It may be distinguished from the last-named substance by its reaction with the salts of lead, not being precipitated from its watery solution by the neutral, but only by the tribasic acetate. If a watery solution, therefore, containing both biliary salts be precipitated by neutral lead acetate, the filtered fluid will contain the taurocholate alone. In alcoholic solution it rotates the plane of polarization toward the right 24.5°. With the exception of glucose, lactose and glycogen, the biliary salts are the only substances known in the animal body which exert a right-handed rotation on polarized light.

The proportion in quantity of the two biliary salts varies somewhat in different cases. Generally the glycocholate may be said to preponderate in the bile of ruminant animals, taurocholate in that of the carnivora. In dog's and cat's bile, the taurocholate exists alone. In human bile both substances may be present, sometimes one being more abundant, sometimes the other; according to some writers the taurocholate existing alone or in larger proportion (Gorup-Besanez, Hoppe-Seyler, Robin, Hardy), according to others the glycocholate (Bischoff, Lossen, Ranke). In the observations of Jacobsen,* on a case of biliary

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* Revue des Sciences Médicales, Paris, 1874, vol. iii., p. 85.

fistula in man, the glycocholate was shown to be a constant ingredient, while the taurocholate was either absent or variable in quantity. We have also found human bile to contain the glycocholate without the taurocholate.

The biliary salts are formed in the tissue of the liver, and are thence discharged with the bile. They are derived, in the opinion of most physiologists, from a transformation of albuminous matters, as indicated by the nitrogen and sulphur which they contain. According to the observations of Ranke on a patient with biliary fistula, the average quantity of the organic acids of the bile thus produced, in a man weighing 65 kilogrammes, would be a little over 15 grammes per day. Although a small amount has been found by Hoppe-Seyler in the feces, this appears to be much less than the total quantity produced in the liver for a corresponding time. Similar observations on animals have also shown that the main part of the biliary salts are not discharged with the feces, but are changed in the intestine, and, probably, reabsorbed under another form by the blood.

Pettenkofer's Test for the Biliary Salts.—The biliary salts, when in considerable quantity, may be recognized by their solubility in water and in absolute alcohol, their insolubility in ether, their form of crystallization, and their reaction with the salts of lead. When present in small proportion they are detected by Pettenkofer's test, which consists in the production of a red color, changing to purple or violet, on the addition of cane sugar and sulphuric acid. The test is applied in the following way: One part of cane sugar is dissolved in four parts of water. Of this liquid, one drop is added to each cubic centimetre of the solution of biliary salts. On treating the mixture with a few drops of pure sulphuric acid, the biliary acids are decomposed, forming cholic acid. If the biliary salts be present in a proportion of not more than one part in 500, the solution remains clear: if in larger quantity, the cholic acid is precipitated, forming a whitish turbidity. This turbidity is again cleared up on the continued addition of sulphuric acid; and in the course of a few minutes a cherry-red color appears, changing rapidly to a violet, and subsequently, if the biliary salts be present in the proportion of one part in 500 or over, to a deep rich purple. In very dilute solutions, the violet or purple color may not be distinctly visible before the end of an hour.

The precautions required in the use of this test are as follows: First, the liquid to be examined should be free from other organic substances, particularly albuminous and coloring matters. For this purpose, it should be evaporated to dryness, the dry residue extracted with absolute alcohol, the alcoholic solution decolorized, if necessary, with animal charcoal, then precipitated with ether in excess, and the ether precipitate dissolved in water. This gives a clear, colorless solution, free from organic contamination. Secondly, as the solution becomes heated by the liberal admixture of sulphuric acid, its temperature should not be allowed to rise above 70° C., nor to fall much below this point. For that purpose, the test-tube may be cooled by occasionally immersing it in cold water. Thirdly, the addition of sulphuric acid should be made slowly, and should be stopped as soon as a red tint begins to show itself, the mixture being left at rest until the violet and purple colors are developed.

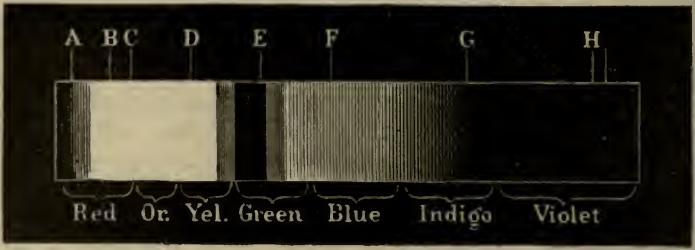
There are various other substances which yield a red, violet, or purple color, when treated with sugar and sulphuric acid. Among these are oleine, oleic acid, ethereal oil, amyl-alcohol, albuminous matters, and the salts of morphine and codeine. Albumen of the blood, white of egg, and the opium alkaloids in the proportion of ten parts per thousand, if treated with Pettenkofer's test, all produce a color undistinguishable from that obtained with the biliary salts. These substances, however, with the exception of morphine, may all be excluded by previously treating the fluid as above described; namely, evaporating to dryness, extracting with alcohol, precipitating with ether, and dissolving the precipitate in water. The salts of morphine might still remain, as they are soluble both in water and in alcohol, and may be precipitated by ether from their alcoholic solution. This substance, however, is very unlikely to be present in an extract of the animal fluids, especially in the proportion of ten parts per thousand.

Pettenkofer's test is a very delicate one. A watery solution of pure sodium glycocholate, made in the proportion of one part to 2,000, yields, at the end of fifteen minutes, a clear violet-pink color, if the test be applied with care; and a solution of sodium taurocholate, in the proportion of one part to 3,000, will give a similar color at the end of an hour. The characters of the test are the same in both cases, as the reaction is really produced by cholic acid, derived from the decomposition of either of the biliary salts.

The *spectrum* of Pettenkofer's test may be of service in distinguishing it from similar reactions produced by other organic substances. If either or both of the biliary salts, dissolved in water, be treated with sugar and sulphuric acid until a violet or purple color is produced, and the colored fluid then placed before the slit of the spectroscope, its spectrum shows a wide and dark absorption band at E, extending from midway between D and E to a quarter part the distance between E and F, the central parts of the band being darker than the edges. Beyond the absorption band, the spectrum is dim, fading gradually, and terminating somewhere about the line G.

When the purple color produced by Pettenkofer's test with the biliary salts is very pronounced, the fluid is usually too opaque for spectroscopic examination, even in a layer of one centimetre; and if diluted with water, its purple color disappears, and it becomes turbid, owing to re-precipitation of the cholic acid. This difficulty may be obviated by making the solution of biliary salts sufficiently dilute in the first instance. A solution of sodium glycocholate, in the proportion of one part to 500, treated with Pettenkofer's test, gives in a few moments a clear violet-pink color, which afterward becomes a rich purple. The purple fluid is so opaque that, when placed before the slit of the spectroscope in a layer of one centimetre, it completely extinguishes everything but the red; and yet it may be diluted with water without showing any turbidity or losing its color. A solution of the above strength is amply sufficient to exhibit Pettenkofer's reaction as well as its spectroscopic characters. If a solution of the biliary salts should prove, when treated by Pettenkofer's test, too opaque for spectroscopic examination, another portion may be reduced, before applying the test, to about the strength of one part to 500. When a strongly colored purple fluid has been rendered turbid and decolorized, as above described, by the addition of water, its transparency and color may be again restored by the addition of sulphuric acid; but this method is less convenient than the former.

Fig. 17.



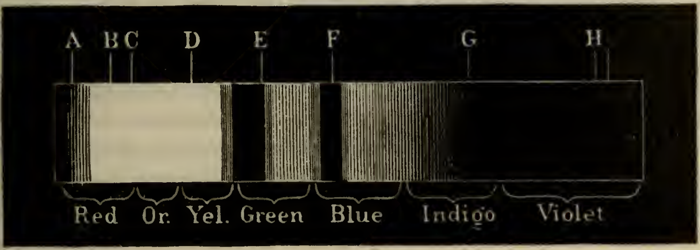
Spectrum of Pettenkofer's Test, with the Biliary Salts in watery solution.

If Pettenkofer's test be applied to the biliary salts in alcoholic solution, its spectrum contains two absorption bands instead of one. The first is situated at E, and is identical with that in a watery solution of the same salts. The second band, at F, is usually rather narrower and fainter than the first, although sometimes the two are of equal intensity.

The pink or purplish-red fluid, produced by Pettenkofer's test with a watery solution of either *codeine* or *morphine*, has a spectrum somewhat similar to that of the biliary salts. If the ruddy color of the fluid be strongly pronounced, its spectrum, even in a layer of one centimetre, is very short, terminating about midway between D and E, or even before that point, showing the red and yellow clear and bright, but very little of the green. If diluted with water, the mixture is not rendered turbid, but its color is reduced, being soon changed to a faint amber, or often to a light apple-green, while the former peculiarities of the spectrum disappear. The best way is to place the fluid before the slit of the spectroscope in a layer of two centimetres before its ruddy hue is fully developed, and while it is still of a light pink. The color then gradually becomes more pronounced, and, when it has attained the proper strength, the spectrum exhibits a certain, though ill-defined absorption band at E. Beyond the band, the spectrum is very dim, terminating gradually between F and G.

The distinction between the spectrum of Pettenkofer's test with biliary salts and that with the opium alkaloids is, that in the former case the absorption band at E is very distinct, and often quite black, when viewed in a layer of two centimetres' thickness; while in the latter it is always dim and ill-defined. With the biliary salts, also, the fluid may often be diluted with its own or even twice its volume of water, and the absorption band still remain visible; but with morphine or codeine a very moderate dilution destroys the character of the spectrum and causes the absorption band to disappear.

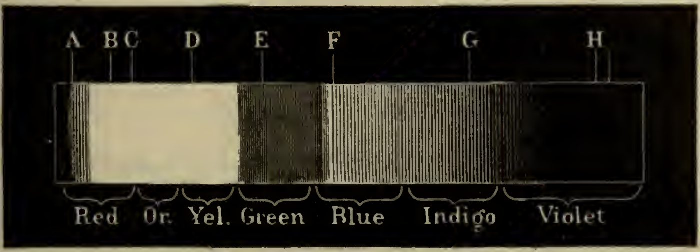
Fig. 18.



Spectrum of Pettenkofer's Test, with the Biliary Salts in alcoholic solution.

The violet-colored fluid produced by Pettenkofer's test with *albumen* has a well-marked and peculiar spectrum, easily distinguishable from that of the biliary salts. If too opaque for spectroscopic examination, it may be diluted with water and afterward cleared up by the further addition of sulphuric acid. It then shows a single absorption band, extending from somewhere about the line E to the line F. In concentrated solutions it may begin considerably to the left of E, and extend thence to F. In those which are more dilute, it may reach only from a little beyond E to F. It is, therefore, always limited on the right by the line F, extending farther toward E and D, according to the degree of concentration of the liquid. Its edges are never very well defined, but are more distinct when the band is narrow than when it is wide. Beyond the band, the refrangible portion of the spectrum is quite dim.

Fig. 19.



Spectrum of Pettenkofer's Test, with albumen.

7. Creatine, $C_4H_9N_3O_2$, from κρέας, flesh.

This is a neutral crystallizable substance, which exists in the muscular tissue, both voluntary and involuntary, of man and animals; its proportion in human muscles being, according to Neubauer,* about two parts per thousand. It has also been found in minute quantity in the blood, the brain, and the kidneys. It is soluble in cold, very readily in hot water, slightly soluble in alcohol, insoluble in ether. From its watery solution it crystallizes in transparent, colorless, rhombic prisms of firm consistency. It is decomposed by a temperature of 100° C. By boiling in acid solutions, or by long-continued boiling in water, it is transformed into another closely related substance, namely, creatinine. If boiled with baryta-water it produces, among other substances, urea, carbonic acid, and ammonia. Creatine is regarded as a product of the metamorphosis of albuminous matters, especially of those existing in muscular tissue. It does not appear in the urine, but undergoes a further transformation, probably into the following substance.

8. Creatinine, $C_4H_7N_3O$,

Is known to exist, with certainty, only in the urine. Although occasionally found in the muscles, it is generally regarded by physiological chemists (Neubauer, Hoppe-Seyler, Gorup-Besanez), not as a normal ingredient of the muscular tissue, but as a product of transformation of the previously existing creatine. It is soluble in water and in alcohol, but only slightly soluble in ether. It crystallizes in colorless, glittering prisms. In solution it has a strongly alkaline reaction, decomposes the combinations of ammonia, and forms with various acids neutral salts.

The chemical relation between these two bodies is such that by hydration or dehydration they may be converted into each other. In the interior of the body creatine is no doubt converted into creatinine, since the former exists normally in the muscles, while the latter is an ingredient of the urine. In this change the elements of water are eliminated as follows:

$$\underset{\text{Creatine.}}{C_4H_9N_3O_2} - H_2O = \underset{\text{Creatinine.}}{C_4H_7N_3O}.$$

Creatine thus represents an intermediate stage of metamorphosis, and finally appears in the urine under the form of creatinine. According to Neubauer, the quantity of creatinine discharged by a healthy man, under ordinary diet, is about one gramme per day.

9. Urea, CH_4N_2O.

This, the most important and well known substance of its class, is the principal solid ingredient of the urine, and the main product of the decomposition of nitrogenous matters in the body. It is most abundant in the urine, where it is present on the average, in man, in the proportion of 26 parts per thousand; while in the blood it amounts to only 0.16 part per thousand. As it makes its appearance in the blood, it is drained away by the kidneys, and thus accumulates in larger

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* Neubauer und Vogel, Analyze des Harns. Wiesbaden, 1872, p. 20.

proportion in the urine. This is shown by the analyses of Picard, who found, in the dog, the proportion of urea in the blood of the renal arteries 0.36 per thousand, in the renal veins 0.18 per thousand.

After extirpation of the kidneys, in the dog,* the urea in the blood of the general circulation increases in twenty-four hours from 2½ to nearly 8 times its former proportion. The same effect is produced by tying the renal arteries, or by ligature of both ureters, which arrests the functional activity of the kidneys. Gréhant corroborated the observations of Picard in regard to a diminished proportion of urea in the blood of the renal vein, as compared with that of the renal artery, in the healthy animal; but after ligature of the ureter, the proportion of urea was no longer diminished while passing through the kidney. It is plain from these experiments that the immediate source of urea is not in the kidneys, but in some other part or parts of the general system. It has been found in the lymph, the aqueous and vitreous humors of the eye, the crystalline lens, the liver and the spleen, and in minute quantity in the perspiration.

Though urea is evidently derived from the nitrogenous organic substances, the exact manner and place of its formation in the body have not been determined. It has been artificially produced by Béchamp† from albuminous matter, placed in contact with potassium permanganate in watery solution, and subjected to a heat of 60° or 80° C. This reaction has been confirmed by Ritter,‡ in whose experiments 30 grammes of albumen furnished 0.09 gramme of urea, and the same quantity of fibrine, 0.07 gramme; while from 30 grammes of gluten, in an average of three experiments, there was obtained 0.27 gramme of urea. This process, however, is not one of simple oxidation, but an oxidation with decomposition, in which various other substances are produced at the same time.

Urea is a colorless, neutral substance, very soluble in water and in boiling alcohol, less so in cold alcohol, nearly insoluble in ether. It crystallizes in four-sided prisms, which are decomposed on being heated above 120° C. Its pure watery solution may be kept without change at ordinary temperatures; but by continued boiling, or by a short boiling in the presence of alkalies, it is decomposed with the production of ammonium carbonate. If heated with water in an hermetically sealed tube to 180° C. it undergoes the same alteration. This change takes place with the assumption of the elements of water, as follows:

$$\underset{\text{Urea.}}{CH_4N_2O} + 2H_2O = \underset{\text{Ammonium carbonate.}}{(NH_4)_2CO_3}.$$

Daily quantity of Urea and its variations.—The quantity of urea

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* Prevost and Dumas, Annales de Chimie et de Physique, Paris, 1823, tome xxiii., p. 90; Ségalas, Journal de Physiologie, tome ii., p. 354; Mitscherlich, Tiedemann and Gmelin, Poggendorf's Annalen, band xxxi., p. 303; Cl. Bernard, Liquides de l'Organisme. Paris, 1859, tome ii., Deuxième Leçon. Gréhant, Centralblatt für die Medicinischen Wissenschaften. Berlin, 1870, p. 249.

† Comptes Rendus de l'Académie des Sciences. Paris, 1870, tome lxx., p. 866.

‡ Comptes Rendus, 1871, lxxiii., p. 1219.

excreted by a healthy man is about 35 grammes per day. This amount varies with the size of the body, the average daily proportion of urea to the weight of the whole body being 0.5 per thousand parts. Lehmann, in experiments on his own person, found the average daily quantity to be 32.5 grammes. Bischoff, by similar experiments, found it to be 35 grammes. Hammond, whose weight was 90 kilogrammes, found it to be 43 grammes. Draper, whose weight was 66 kilogrammes, found it 26.5 grammes.

It has been shown by Draper,* and confirmed by other observers, that there is a *diurnal* variation in the normal quantity of urea. A smaller quantity is produced during the night than during the day; and this difference exists even in patients confined to the bed during the whole twenty-four hours, as in the case of a man with fracture of the leg. Its production is less abundant during the forenoon than in the afternoon or evening, the maximum occurring from 3 to 5 hours after the principal meal of the day.

An important variation in the daily excretion of urea is that which corresponds with the kind and quantity of the food. Urea is the principal representative of the decomposition of the nitrogenous ingredients of the body, as it is the only substance containing nitrogen which is discharged in any considerable amount by the excretions. A comparison of the nitrogen contained in the daily food with that discharged from the body in various forms shows that fully 85 per cent. reappears as an ingredient of the urea; the remaining 15 per cent. being contained in the uric and hippuric acids and creatinine of the urine, and in the nitrogenous matters of the feces.

All observers agree that the quantity of urea excreted varies in proportion to the nitrogenous matters contained in the food. Lehmann† found in experiments on his own person, that the daily amount of urea was increased by animal food, diminished by vegetable food, and reduced to its minimum by a diet consisting exclusively of non-nitrogenous matters, such as starch, sugar, and fat. The comparative results were as follows:

Kind of diet.	Daily quantity of urea.
Mixed	32.5 grammes.
Animal	53.2 "
Vegetable	22.5 "
Non-nitrogenous	15.4 "

It also appears, from the observations of Mahomed,‡ that the influence of a change of diet in this respect is manifested very rapidly; twenty-four hours of a non-nitrogenous diet being sufficient to reduce the excretion of urea 50 per cent., while it is restored to its ordinary standard within three or four hours after the use of animal food.

Urea, however, does not depend exclusively on the direct trans-

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* New York Journal of Medicine, March, 1856.

† Physiological Chemistry, Sydenham Edition. London, 1853, vol. ii., p. 450.

‡ Pavy, Food and Dietetics, Philadelphia Edition, 1874, pp. 79–81.

formation of nitrogenous matters in the food, but is also derived from the metamorphosis of the more permanent constituents of the body; since it continues to be discharged, though in diminished quantity when no food is taken. Lehmann found as much urea in the urine after twenty-four hours of abstinence from all food, as after a diet of non-nitrogenous matters. In the dog, when subjected to entire abstinence, the urea is reduced in three or four days nearly to one-third its former quantity, but is still present in about the same proportion at the end of seven days. In the experiments of Parkes on a man subjected to purely non-nitrogenous diet, the daily excretion of urea fell on the second day to 12 grammes, but afterward remained nearly uniform, at rather more than half that quantity, and on the fifth day still amounted to 7 grammes. Urea has also been found by Lassaigne in the urine of man after continued abstinence from food for fourteen days.

Very contradictory statements have been made in regard to the influence of muscular exertion on the production of urea. By some observers (Lehmann, Flint, Weigelin, Parkes, and Vogel) the urea has been found to be increased during or after unusual bodily activity; by others (Fick and Wislicenus, Voit, Ranke) it has been denied that muscular exertion causes such an effect. This discrepancy has resulted mainly from not taking into account the increase or diminution of nitrogenous food simultaneously with the periods of muscular rest or activity. There can be no doubt, since the observations of Flint* on the pedestrian Weston, afterward repeated by Pavy,† on the same person, with essentially similar results, that the production of urea in man is considerably increased by muscular exertion, and that this increase is over and above what can be accounted for by the nitrogenous food consumed. It must, therefore, be attributed to the functional activity of the muscular system; and as this system forms no less than 40 per cent., by weight, of the entire frame, it will account for a considerable portion of the urea produced. It is, also, a matter of common experience, both for man and animals, that continued and laborious muscular activity requires a corresponding supply of nitrogenous food; and the final result of the internal metamorphosis of such substances is mainly represented by urea.

10. Sodium Urate, $C_5H_3N_4O_3Na$.

As its name indicates, this is a saline body, consisting of a nitrogenous organic acid, namely, *uric acid* ($C_5H_4N_4O_3$), in union with sodium. A portion is also in combination with potassium, but the sodium salt is in much the greater quantity. The urates are found normally only in the urine, where they exist in the proportion of about 1.45 parts per thousand. The entire quantity of uric acid excreted by a healthy, full-grown man, is about 0.7 gramme per day. It is, therefore, very much less abundant than urea; and, according to the researches of Ranke,

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* New York Medical Journal, June, 1871.

† London Lancet, 1876, vol. ii., p. 848.

the proportion between the two is very constant, their relative quantity in the same individual being nearly always—

Uric acid	1 part.
Urea	45 parts.

Uric acid is a colorless, crystallizable substance, very slightly soluble in cold or hot water, insoluble in alcohol and in ether. It is less easily decomposed than urea, remaining for a long time unchanged under ordinary conditions. If treated with concentrated sulphuric acid it is decomposed, with the production of ammonia and carbonic acid. If boiled with dilute nitric acid, it dissolves with a yellow color and abundant liberation of gas-bubbles; and, on evaporation, the solution leaves a brilliant red stain, which is changed to purple by the addition of ammonia water. This is known as the "murexide test" for uric acid or the urates.

Uric acid, like urea, is formed within the body by the metamorphosis of nitrogenous organic substances. It is most abundant under the use of animal food, is diminished by a vegetable diet, and is reduced to a minimum, though it does not entirely disappear, during complete abstinence. It is also increased by muscular exercise and diminished by repose. It is this substance which indirectly causes the acid reaction of the urine. It is nowhere present normally in a free form, being by itself exceedingly insoluble; but simultaneously with its production it unites with part of the alkaline base of the phosphates, thus becoming sodium urate, which is soluble and neutral in reaction, and giving rise to sodium biphosphate, which communicates to the urine its acid reaction.

11. Sodium Hippurate, $C_9H_8NO_3Na$.

This is also a saline body, formed by the union of sodium with a nitrogenous organic acid, namely, *hippuric acid* ($C_9H_9NO_3$), so called because first discovered in the urine of the horse. It is comparatively abundant in most herbivorous animals, especially the horse, ox, sheep, goat, elephant, camel, and rabbit; while it is absent, or nearly so, in the carnivorous animals. In human urine, under an ordinary mixed diet, it is constantly present, amounting to about 0.35 gramme per day, or about one-half the quantity of uric acid. It increases perceptibly under a vegetable diet, and diminishes or disappears under the exclusive use of animal food. It thus alternates in quantity, under these circumstances, with uric acid. In the urine of the horse, which normally contains hippuric acid, after continued abstinence from food, this substance ceases to appear and uric acid takes its place. Herbivorous animals, when deprived of food, are placed in the condition of carnivora, since the ingredients of the urine must then be derived from the metamorphosis of their own substance. In the calf, while living on the milk of its dam, the urine contains uric acid; after the animal is weaned and begins to live on vegetable food, the uric acid disappears, and the urine contains salts of hippuric acid.

CHAPTER VII.

FOOD.

UNDER the term "food" are included all substances, solid or liquid, necessary for nutrition. The first act of this process is the appropriation from without of the materials of the living frame, or of other substances which may be converted into them. Like the tissues and the fluids, therefore, the food contains various ingredients, both organic and inorganic; and the first important fact with regard to them is that *no single class of these substances is sufficient to sustain life*, but that several must be supplied in due proportion, to maintain the body in a healthy condition.

Inorganic Ingredients of the Food.

Inorganic substances, although they afford the necessary materials for vegetation, are not sufficient for the nourishment of animals, which depend for their support upon elements already combined in the organic form. The inorganic matters are nevertheless essential to animal life, and require to be supplied in sufficient quantity to maintain their natural proportion in the animal solids and fluids. As they are generally exempt from alteration in the interior of the body, and are absorbed, deposited, and expelled unchanged, each one, as a rule, requires to be present under its own form, and in sufficient quantity, in the food. This is especially true of water and sodium chloride, both of which enter and leave the system in abundant daily quantity; and of the calcareous salts which, during the growth and ossification of the skeleton, are largely deposited in the osseous tissue. The alkaline carbonates, phosphates, and sulphates are partly formed within the system during the metamorphosis or decomposition of organic substances; but their elements must of course enter the body in some form, in order to enable these changes to be accomplished.

Since water enters into the composition of every part of the body, it is an important ingredient of the food. In man, it is probably the *most* important substance to be supplied with constancy and regularity, and the system suffers more rapidly when deprived of fluids, than when the supply of solid food only is withdrawn. Magendie found, in his experiments on dogs subjected to inanition,* that the animals supplied with water alone lived six, eight, or even ten days longer

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* Comptes Rendus de l'Académie des Sciences. Paris, tome xiii., p. 256.

than those deprived of both solids and liquids. Sodium chloride, also, is usually added to the food in considerable quantity, and requires to be supplied as a condiment with some regularity; while the remaining inorganic materials, such as calcareous salts, and the alkaline phosphates and sulphates, occur naturally in sufficient quantity in most articles of food.

The entire quantity of mineral substances discharged daily by a healthy adult, by both the urine and perspiration, averages as follows:

QUANTITY OF MINERAL MATTERS DISCHARGED PER DAY.

Sodium and potassium chlorides . . .	15.0	grammes.
Calcareous and magnesian phosphates . .	1.0	"
Sodium and potassium phosphates . . .	4.5	"
Sodium and potassium sulphates . . .	4.0	"
	24.5	"

According to the average dietaries for adults, in full health, collected by Playfair,* about 20 grammes of mineral matter are daily introduced with the food. The remainder is accounted for by the phosphates and sulphates formed within the system as above described.

Non-Nitrogenous Organic Ingredients of the Food.

These substances, so far as they enter into the composition of the food, are divided into two natural groups, namely, *carbohydrates*, including starch and sugar, and *fats*, including all varieties of oleaginous matter. Since starch is converted into glucose in the digestive process, these two substances may be regarded as having the same nutritive value. They occur abundantly only in vegetable products, and the herbivorous animals alone consume them in considerable quantity in their food; while the carnivora obtain a comparatively small proportion of glycogen and glucose in the tissues and juices upon which they feed. For man the natural diet is a mixed regimen of animal and vegetable food; and it is invariably found that a continued privation of vegetable substances produces a craving for carbohydrates, which indicates their necessity for healthy nutrition.

A similar question has arisen with regard to oleaginous matters. Are these substances indispensable in the food, or may they be replaced by starch or sugar? It has already been seen, from the experiments of Boussingault, that a certain amount of fat is produced in the body over and above that taken with the food; and it appears also that a regimen abounding in saccharine substances is favorable to the production of fat. It is probable, therefore, that the materials for the production of fat may be derived, either directly or indirectly, from saccharine matters. But saccharine matters alone are not sufficient. Dumas and Milne-Edwards† found that bees, fed on pure sugar, soon cease to work, and sometimes perish in considerable numbers; but if

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* London Chemical News, May 12, 1865.

† Annales de Chimie et de Physique, 3d series, tome xiv., p. 400.

fed with honey, which contains some waxy and other matters beside sugar, they thrive upon it; and produce, in a given time, a larger quantity of fat than was contained in the food.

The same thing was established by Boussingault with regard to starchy matters. He found that in fattening pigs, though the quantity of fat accumulated by the animal considerably exceeded that contained in the food, yet fat must enter to some extent into its composition to maintain the animal in good condition; for pigs, fed on boiled potatoes alone (an article abounding in starch but nearly destitute of oily matter), fattened slowly and with difficulty; while those fed on potatoes mixed with a greasy fluid fattened readily, and accumulated much more fat than was contained in the food. In order, therefore, that an animal become fattened, it must be supplied not only with the materials of the fat itself, but with everything else necessary to maintain the body in a healthy condition. Oleaginous matter is one of these substances. We cannot assume that the fats taken in with the food are simply absorbed, and deposited unchanged in the system. They may be in great measure decomposed or transformed in the process of nutrition; those which appear as constituents of the tissues being products of new formation, derived perhaps from a variety of sources.

It is certain that either one or the other of these two groups of substances, saccharine or oleaginous, must enter into the composition of the food; and furthermore, that, though oily matter may sometimes be produced in the body from the sugars, it is also necessary that it be supplied under its own form. In the food of man they are naturally associated in many vegetable alimentary matters; while the fats are supplied in addition from a variety of animal substances.

But neither the carbohydrates nor the fats, alone or associated with each other, are sufficient for nutrition. Magendie found that dogs, fed exclusively on starch or sugar, perished after a short time with symptoms of profound disturbance of the nutritive functions. An exclusive diet of butter or lard had a similar effect. The animal became exceedingly debilitated, though without much emaciation; and after death the internal organs and tissues were found infiltrated with oil. Boussingault* performed a similar experiment, with like result, upon a duck, which was kept on an exclusive regimen of 90 to 100 grammes of butter per day. At the end of three weeks it died of inanition, although every part of the body was saturated with oily matter.

Lehmann was led to the same result by experiments upon himself, while investigating the effect produced on the urine by different kinds of food.† He confined himself first to a purely animal diet for three weeks, afterward to a purely vegetable diet for sixteen days, without marked inconvenience. He then put himself upon a regimen of non-nitrogenous substances, starch, sugar, gum, and oil, but was only

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* Chimie Agricole. Paris, 1854, p. 166.

† Journal für praktische Chemie, Band xxvii., p. 257.

able to continue this diet for two, or at most for three days, owing to disturbance of the general health. The unpleasant symptoms disappeared on his return to a mixed diet. In some instances a restricted diet of this kind has been borne for a longer time. Parkes* kept two soldiers on non-nitrogenous food for five consecutive days without their exhibiting serious signs of physical exhaustion. Hammond,† in experiments upon himself, lived for ten days on a diet of boiled starch and water. After the third day, however, the general health began to deteriorate, and became much disturbed before the termination of the experiment; the prominent symptoms being debility, headache, pyrosis, and palpitation. After the starchy diet was abandoned, it required some days to restore the health to its usual condition.

Nitrogenous Ingredients of the Food.

The nitrogenous or albumenoid matters enter so largely into the constitution of the animal tissues and fluids, that their importance, as elements of the food, is easily understood. No food can be long nutritious, unless a certain proportion of these substances be present. Owing to their abundant quantity as ingredients of the body, their absence from the food is more speedily felt than that of any other substance except water. Albuminous matters, however, when taken alone, are no more capable of supporting life indefinitely than the rest. It was found in the experiments of the French "Gelatine Commission"‡ that animals fed on pure fibrine and albumen, as well as those fed on gelatine, become, after a short time, much enfeebled, refuse the food offered, or take it with reluctance, and finally die of inanition. This result has been explained by supposing that these substances excite after a time such disgust that they are either no longer taken, or if taken are not digested. But this is simply an indication that the substances used are insufficient and finally useless as articles of food, and that the system demands other materials for its nourishment. It is well described by Magendie, in the report of the commission above alluded to, while detailing his investigations on the nutritive qualities of gelatine. "The result," he says, "of these first trials was that pure gelatine was not to the taste of the dogs experimented on. Some of them suffered the pangs of hunger with the gelatine within their reach, and would not touch it; others tasted it, but would not eat; others still devoured a certain quantity once or twice, and then obstinately refused to make any further use of it."

In one instance, Magendie succeeded in inducing a dog to take a considerable quantity of pure fibrine daily throughout the whole course of the experiment; but the animal nevertheless became emaciated, and died at last with symptoms of inanition.

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* Proceedings of the Royal Society of London, March 2d, 1871.

† Experimental Researches, being the Prize Essay of the American Medical Association for 1857.

‡ Comptes Rendus de l'Académie des Sciences. Paris, 1841, tom. xiii., p. 267.

It is evident, therefore, that no single organic substance, nor even any one class alone, is sufficient for nutrition. The albuminous matters are first in importance because they constitute the largest part of the mass of the body; and exhaustion follows more rapidly when they are withheld than when the animal is deprived of other kinds of alimentary matter. But starchy and oleaginous substances are also requisite; and the body feels their want sooner or later, though plentifully supplied with albuminous food. Finally, the inorganic saline matters, in smaller quantity, are also necessary to the maintenance of life. In order that the animal tissues and fluids remain healthy, and perform their proper functions, they must be supplied with all the ingredients necessary to their constitution; and a man may be starved to death at last by depriving him of sodium chloride or lime phosphate as surely, though not so rapidly, as if he were deprived of albumen or oil.

Composition of Different Articles of Food.

In the most valuable and nutritious kinds of food, adopted by the universal and instinctive choice of man, the carbo-hydrates, fats, albuminous and inorganic matters are all usually present in certain proportions.

Milk.—In milk, the first food supplied to the infant, and largely employed in various culinary operations, all the important groups of nutritive substances are represented. It is a white, opaque fluid, consisting, 1st, of a serous portion, with albuminous matters, sugar, and mineral salts in solution, and 2d, of fatty globules suspended in the watery liquid. It is this mixture of oleaginous particles with a serous fluid which gives to the milk its opacity and its white color. Its richness in fatty matter may therefore be estimated from these physical qualities. The ingredients in cow's milk are present, according to Payen, in the following proportions:

Composition of Cow's Milk in 1,000 parts.

Water	864
Albuminous matter	43
Sugar of milk	52
Fat	37
Mineral salts	4
	1,000

Cow's milk resembles human milk in its general characters, but contains a larger proportion of solid ingredients, especially of the nitrogenous and saccharine matters, fat being present in nearly the same amount in each. Sheep and goat's milk is richer in both nitrogenous and fatty matters; while the milk of the ass and the mare contains a greater abundance of sugar, but is comparatively poor in nitrogenous matter and fat. The nitrogenous matter of milk consists almost entirely of caseine, associated with a small proportion of albumen. Owing to the relative quantity of these two substances, milk does not solidify on boiling, but merely covers itself with a thin pellicle of coagulated albumen, the caseine remaining liquid. The addition of any acid, however, such as acetic or tartaric acid, will precipitate the caseine and curdle the milk. If milk be allowed to remain exposed to the air at a moderately warm temperature, it curdles spontaneously, owing to the development of lactic acid, from transformation of its sugar; and the same change will occur instantaneously from electric disturbance, during a thunder-storm.

The caseine of milk, artificially coagulated by the action of rennet, constitutes *cheese.* Rennet is the dried contents and mucous membrane of the stomach of the calf, the animal being killed and the stomach taken out while digestion is in full activity and the gastric fluids abundantly secreted. An infusion of this substance even in small quantity, added to fresh milk at the temperature of 30° C. produces coagulation in fifteen or twenty minutes. The coagulum is drained from the watery serum or "whey," and afterward pressed into the form of cheese. The variety in consistency and flavor of different cheeses depends mainly on the proportion of fatty matter retained in the coagulum, and on certain slow changes, in the nature of fermentations, which go on in it subsequently.

The fatty matter of milk is suspended in its serous portion under the form of minute spheroidal masses. These masses or "milk-globules" are not quite fluid at ordinary temperatures, but have a semi-solid consistency owing to their containing a considerable proportion of palmitine. The fat globules, separated by churning from the other ingredients of the milk, and united into a coherent mass, constitute *butter.* This substance, accordingly, represents the oleaginous ingredients of the milk; and when purified from the watery portions entangled with it, consists mainly of palmitine and oleine, with certain flavoring ingredients, the principal of which has received the name of "butyrine." These substances are usually mingled in the following proportions:

Palmitine	68	parts.
Oleine	30	"
Butyrine and other flavoring matters	2	"
	100	

When well prepared and in good condition, butter constitutes one of the most valuable and easily assimilated forms of oleaginous food. If contaminated with the nitrogenous matter of the milk, its fatty ingredients after a time become decomposed with the development of volatile fatty acids; in which condition it is said to be "rancid," and is no longer fit for food.

Bread.—The cereal grains resemble each other more or less in their constitution, all of them containing starch, nitrogenous matter, dextrine or sugar, fat, and mineral salts in various proportions. Wheat is distinguished by containing a larger quantity of nitrogenous matter as compared with the other ingredients, and by the peculiarly adhesive quality of this substance, which has received accordingly the name of "gluten." The different grains in common use for food have, when dry, the following average composition, according to Payen.

COMPOSITION OF THE CEREAL GRAINS.

	Nitrogenous Matter.	Starch.	Dextrine, etc.	Fat.	Cellulose.	Mineral Salts.
Wheat	18.00	66.80	7.50	2.10	3.10	2.50
Rye	12.50	64.65	14.90	2.25	3.10	2.60
Barley	12.96	66.43	10.00	2.76	4.75	3.10
Oats	14.39	60.59	9.25	5.50	7.06	3.25
Indian corn . . .	12.50	67.55	4.00	8.80	5.90	1.25
Rice	7.55	88.65	1.00	0.80	1.10	0.90

Thus, of the cereal grains, oats contain, next to wheat, the largest proportion of nitrogenous matters; but they also contain a considerable abundance of cellulose, or indigestible vegetable tissue, which interferes with their nutritive quality as human food. Indian corn is especially rich in fatty ingredients, while rice consists mainly of starch, and is the poorest of all in both nitrogenous and fatty ingredients.

Wheat is more valuable than the other cereal grains for making bread, not only on account of its larger proportion of albuminous matter, but also on account of the peculiar glutinous quality of this ingredient, which is useful in giving to the dough a proper consistency.

In preparing the wheat, the grains are first cleansed from husks and adherent foreign material, ground into meal, and the finer and whiter portions from the interior of the grain separated, by sifting and bolting, from the coarser external parts, or bran. Thus purified, the flour consists of starch, gluten, diastase, dextrine, a little fat, sometimes a trace of sugar, mineral salts, and about 15 per cent. of water, which is never wholly expelled by ordinary drying. For making into bread, the flour is mixed with about one-half its weight of water, and kneaded into a flexible dough of uniform consistency. The next process is the fermentation of the dough. For this purpose a little yeast is incorporated with it, and the mixture allowed to remain for a few hours at a temperature of about 25° C. During this time the sugar originally present in the flour, and that produced from the starch and dextrine by the action of the diastase, passes into fermentation under the influence of the yeast, and is transformed into alcohol and carbonic acid. The alcohol is dissipated by evaporation; but the carbonic acid, generated in small gas-bubbles, is entangled by the tenacious gluten of the flour, and the dough is thus puffed up into a spongy, reticulated mass. When the fermentation of the dough is completed, it is placed in ovens, and baked at a temperature of 210° C. The effect of this is to cook the glutinous part of the dough, communicating to it an agreeable flavor, and at the same time solidifying it; so that the baked loaf, when cut open, retains its spongy texture. It is thus made easy of mastication, and readily permeable by the digestive fluids. The spongy texture acquired by bread is the main object of its fermentation, although an agreeable flavor is also developed by the process, which does not exist in unfermented bread. The interior of the loaf, in baking, does not rise above 100° C.; the exterior, which is subjected to a higher temperature, becomes covered with a crust of partially torrefied starch or dextrine, and caramelized sugar. The interior of the loaf also usually retains a little glucose, not destroyed in the process of fermentation. A considerable portion of the water which was mixed with the flour remains united with its organic ingredients; so that 100 parts of flour will usually yield, after baking, 130 parts, by weight, of bread.

Wheaten bread thus prepared has the following average composition:

COMPOSITION OF WHEATEN BREAD.

Starchy matters (starch, dextrine, glucose)	56.7
Albuminous matter (gluten, etc.)	7.0
Fatty matter	1.3
Mineral matter (calcareous, magnesian, and alkaline salts)	1.0
Water	34.0
	100.0

Thus, while bread contains an abundance of albuminous and starchy matter, it is deficient in fat; and instinct leads us to take with it butter, fat bacon, or some other form of oleaginous food.

The good quality of bread, aside from that of the flour from which it is made, depends mainly on the process of fermentation. If this be incomplete, the bread is heavy, and not sufficiently reticulated in texture. If too long continued, it passes into an acid fermentation, and develops a sour taste. When properly fermented, the bread is uniformly light and spongy, and has no acid reaction.

Meat.—The muscular flesh of various animals affords the most valuable and nutritious kinds of food, among which beef, mutton, and venison hold the highest place. The muscular fibre itself consists almost exclusively of nitrogenous matters, but in point of fact the flesh used for food is always accompanied with more or less adipose tissue, and even when freed from visible fat, it always contains, according to Payen and Pavy, more or less oleaginous matter entangled with its fibres. In various kinds of meat, and even in that from different parts of the same animal, the proportion of fat will vary considerably; but it was found by Pavy, in one of the best and most commonly used portions of beef, to amount to about 5 per cent. of the whole.

COMPOSITION OF BEEF FLESH.

Water	77.5
Albuminous matter	16.0
Fat	5.0
Mineral salts	1.5
	100.0

The mineral matters consist of alkaline chlorides and phosphates, with phosphates of lime and magnesia.

In cooking meat by roasting or broiling, the external parts are exposed to a rapid heat of 120° or 130° C. by which their albuminous ingredients are coagulated, their coloring matter turned brown, and a characteristic flavor developed. The interior, which does not rise above 65° C. remains red and juicy, its fluids being protected from evaporation by the coagulation of the outer portions. In boiling, where the meat is cooked by contact with the boiling water, none of it can rise higher than 100° C., but this temperature may penetrate through the whole of its substance, producing a uniform decolorization. Notwithstanding the coagulation of the albuminous liquids, the fibrous connective tissues are gelatinized, and the muscular flesh thus partially softened and disintegrated. On the whole, the effect of cooking upon meat is to increase the consistency of its albuminous ingredients, its principal benefit being the attractive flavor developed by heat, and an increased digestibility from the same cause. By either method, meat loses in cooking from 25 to 30 per cent. of its weight, principally by the escape of water and liquefied fat.

Eggs.—The eggs of various animals are employed for food, as those of the common fowl, the duck, goose, turkey, sea-fowl, turtles, and many fish. Those of the common fowl may be considered as representing the general qualities of this kind of nutriment. They consist of the globular "yolk," surrounded by a layer of albumen or "white." The composition of these two portions is nearly the same, excepting that the yolk contains a larger proportion of solids, and particularly of fatty matter, which gives to it its yellow color and rich flavor. A comparative analysis of the yolk and white is as follows:

Composition of the Fowl's Egg.

	Yolk.	White.
Albuminous matter	16.0	20.4
Fat	30.7	
Mineral salts	1.3	1.6
Water	52.0	78.0
	100.0	100.0

The mineral matters consist mainly of sodium and potassium chlorides, potassium sulphate, and lime and magnesium phosphates. Of the entire contents of the egg, exclusive of shell, the yolk constitutes one-third and the white two-thirds. Cooking produces but little effect upon eggs except to coagulate their albuminous matters, developing only a slight flavor under the influence of heat.

Vegetables.—Of the different vegetables used as food, some are valuable for their starchy and albuminous ingredients, others mainly for their saccharine and watery juices. The former are nutritious in the ordinary sense of the word, though much less so than bread or animal food; the latter are useful for supplying certain materials contained in fresh vegetable juices, which are essential to the maintenance of health. The most important of the first group are represented by the potato and the leguminous seeds. The tuber of the potato abounds in starch, but is poor in other nutritive ingredients.

Composition of the Potato.

Starch	20.0
Albuminous matter	2.5
Sugar and gum	1.1
Fatty matter	0.1
Cellulose	1.0
Mineral and vegetable salts	1.3
Water	74.0
	100.0

The leguminous seeds, on the other hand, contain an abundance of albuminous matter, similar to the caseine of milk, and called "legumine."

Composition of White Beans.

Starch	55.7
Albuminous matter	25.5
Fatty matter	2.8
Cellulose	2.9
Mineral salts	3.2
Water	9.9
	100.0

The composition of dried peas is very similar to the above, the starchy matters being present in rather larger, the albuminous ingredients in rather smaller proportion. Notwithstanding the abundance of nitrogenous matter in leguminous seeds, its quality is inferior to that contained in the cereal grains. Peas and beans also have a texture which renders them comparatively difficult of digestion, and requires long boiling to fit them for use as food. The same is true of many juicy and saccharine roots, such as beets and parsnips, which appear to have a comparatively soft consistency, but which nevertheless need prolonged boiling. The effect of cooking, upon vegetables, is generally to disintegrate and soften their texture, and particularly, by the aid of heat and moisture, to bring their starchy ingredients into a pasty condition. Raw starch is nearly or quite indigestible by man, and if taken into the stomach will often pass unchanged through the bowels; but when cooked it is transformed into glucose by the digestive fluids. It is for this reason that starchy vegetables require more thorough cooking than most kinds of animal food.

Beside the more solid kinds of vegetable food, many of the pulpy and succulent fruits and herbaceous substances are valuable as an addition to the nutritive regimen—celery, lettuce, parsley, spinach, with all the sweet fruits and melons, being used with advantage either in the raw or cooked form. They introduce into the system salts of the vegetable acids, such as malates, tartrates, and citrates, the privation of which for a long time is one of the inducing causes of scurvy.

It is evident, therefore, that the nutritive value of any article of food does not depend on its containing either one of the alimentary substances in large quantity, but upon its containing them mingled in the proportions requisite for nutrition. What these proportions are cannot be determined from chemical analysis, nor from any other data than those of observation and experiment.

Requisite Quantity of Food and of its Different Ingredients.

The entire quantity of food required per day varies with the circumstances of the individual, such as the size and weight of the body, the development of the muscular system, the temperature, and especially the amount of physical activity. More food is required, on the average, in cold than in warm weather, more by persons of a muscular than by those of an adipose or phlegmatic constitution, more in a condition of exertion than in one of repose. Even the proportion of different classes of proximate principles required for nutrition varies according to special conditions. When the individual is perfectly healthy, and can supply himself with any kind of nourishment desired, the natural demands of the appetite afford the surest criterion for both the quantity and quality of food to be used. But provision must often be made for supplies to last over a considerable period, as in military or exploring expeditions, or for the inmates of hospitals or asylums where the diet must be regulated to a great extent on a uniform plan. It, therefore, becomes important to know both the quantity and kind of food necessary for the support of life.

The standard adopted for this estimate is that of a healthy adult man, employed in active but not exhausting occupation. The amount requisite will be found to vary in either direction from this standard, according to the circumstances above mentioned. The average requirements, as given by different authors, do not vary materially from each other in any essential particular. According to our own observations, a man in full health, taking active exercise in the open air, and restricted to a diet of bread, fresh meat, and butter, with water and coffee for drink, consumes the following quantities per day:

QUANTITY OF FOOD REQUIRED PER DAY.

Meat	453	grammes.
Bread	540	"
Butter or fat	100	"
Water	1,530	"

This represents the daily quantity of food and the proportions of its different kinds, when composed of such materials as are most nutritious, and of the most uniform composition. For the continued maintenance of health and strength in a working condition, other articles, such as fresh vegetables, sugar, milk, fruit, etc., should be mingled with the above, in a variety of proportions; but there is no doubt that bread and fresh meat, with a certain quantity of fat, will prove sufficient for the wants of the system, for a longer time than any other articles of food.

Such a diet affords the best means of ascertaining the absolute and relative quantities of the different ingredients required for food. If we take the average composition of meat and bread, and estimate their albuminous, starchy, and saline matters, together with the water contained in both solid and liquid food, we find that the daily ration is composed nearly as follows:

Albuminous matter	130	grammes.
Starch and sugar	300	"
Fat	100	"
Mineral salts	20	"
Water	2,000	"

Of the mineral salts, nearly eight grammes are naturally contained in the substances used for food and drink; the remainder consists of sodium chloride, artificially added to the food, or used in its preparation.

The proportion in which the *albuminous* and the *non-nitrogenous* principles should be mingled in the food is of considerable importance, and this proportion has been determined within very accurate limits. In making such an estimate it is necessary to include the carbohydrates and fats under the same head; but the fats are properly regarded as having a different alimentary value from the carbohydrates. This depends on the fact that the final result of the transformation in the living body of all the non-nitrogenous substances is carbonic acid and water, thus representing a process of oxidation, the necessary oxygen for which is introduced with the inspired air. But the capacity for oxidation of the fats is greater than that of the carbohydrates, as shown by the relative proportion of their constituent elements.

$$\begin{array}{l} \text{The composition, by weight,} \\ \text{of starch } (C_6H_{10}O_5) \text{ is} \end{array} \left\{\begin{array}{lr} C & 72 \\ H & 10 \\ O & \underline{80} \\ & 162 \end{array}\right. \text{ or in 100 parts. } \begin{array}{lr} C & 44.47 \\ H & 6.17 \\ O & \underline{49.36} \\ & 100.00 \end{array}$$

Here the oxygen is already present in sufficient proportion to saturate all the hydrogen by the formation of water; while the 44.47 parts of carbon will unite with 118.58 parts of oxygen to form carbonic acid.

On the other hand, if we take palmitine as representing the average constitution of the fats, we have—

$$\begin{array}{l} \text{The composition, by weight,} \\ \text{of fat } (C_{51}H_{98}O_6) \text{ is} \end{array} \left\{\begin{array}{lr} C & 612 \\ H & 98 \\ O & \underline{96} \\ & 806 \end{array}\right. \text{ or in 100 parts. } \begin{array}{lr} C & 75.93 \\ H & 12.15 \\ O & \underline{11.92} \\ & 100.00 \end{array}$$

Here the oxygen is present in much diminished proportion; and, for complete oxidation of the fat, to form carbonic acid and water, the 75.93 parts of carbon will require 202.48 parts of oxygen, and the 12.15 parts of hydrogen will need 85.28 additional, over and above the 11.92 parts of oxygen already present. Thus the quantities of oxygen appropriated during complete oxidation, by starch and fat respectively, are as follows:

OXYGEN REQUIRED FOR THE COMPLETE OXIDATION OF

100 parts of starch	118.58
" " fat	287.76

A fatty substance, therefore, has a capacity for the production of carbonic acid and water, by oxidation, about 2.4 times greater than that of starch. In estimating, accordingly, the requisite quantity of all the non-nitrogenous matters taken together, the fat is calculated as starch; one part of fat being reckoned as 2.4 parts of starch. This quantity, added to that of the carbohydrates in the food, is called the "starch-equivalent" of the non-nitrogenous matters.

But if we compare the consumption of non-nitrogenous substances, on this basis, with that of albuminous matter, the latter should also be reduced to its "starch-equivalent." After eliminating from albumen all its nitrogen under the form of urea, its remaining constituents still have a higher capacity for oxidation than a corresponding weight of starch; the exact relations of the two being as follows:

OXYGEN REQUIRED FOR THE COMPLETE OXIDATION OF

100 parts of starch	118.58
" " albumen	154.07

Albumen, consequently, without its urea, has a capacity for oxidation 1.3 times as great as that of starch.

When compared in this way, the albuminous matters are found to constitute 22 per cent., and the non-nitrogenous matters 78 per cent. of the entire food; that is, the quantity of non-nitrogenous matter is to that of albuminous matter as 3.55 to 1.

This proportion varies to some extent with the age and condition of the individual. In human milk, which at first forms the exclusive food of the infant, according to the average analyses of Simon, Vernois, and Becquerel, as given by Milne Edwards, the non-nitrogenous matters are to the albuminous ingredients as 2.27 to 1. In cow's milk, upon which the young calf is sustained, the proportion is 2.52 to 1; while in hay and green grass, the food of the adult animal, it is 7.14 and 9.01 to 1. The larger proportion of albuminous matter in the food at an early age is evidently connected with the growth then taking place. As the albuminous matters constitute the larger part of the solid ingredients of the body, the increase in weight during the growing period demands a corresponding supply of these substances in the food.

There is also evidence that the requisite proportion of nitrogenous matter varies with the amount of physical activity. A condition of bare subsistence may be maintained upon a diet in which the albuminous substances are in smaller, and the non-nitrogenous matters in larger proportion; but when the system is called upon for a greater amount of muscular exertion, the proportion of albuminous matters must be increased. This is well known in regard to horses and working-cattle generally. In a state of comparative inactivity they may be supported mainly upon grass or hay, in which the proportion of nitrogenous to non-nitrogenous matter is not more than 1 to 7.14; but when employed in active labor they require a liberal supply of oats, in which the proportion is as 1 to 5.49. In Playfair's diet tables, which were collected from a variety of sources, including those of prisons and infirmaries, those of the American and European armies during peace and in active service, and of certain hard-working laborers, the increase of albuminous matter, with increased labor, is a marked feature. While in a bare subsistence diet the proportion of albuminous to non-nitrogenous matter is as 1 to 4.52, in that of active laborers it is as 1 to 3.34. The following table will show the relative increase of the two kinds of food under different conditions of exercise, as calculated from Playfair's data.

RELATIVE INCREASE, UNDER DIFFERENT CONDITIONS, OF ALBUMINOUS AND NON-NITROGENOUS MATTERS IN THE FOOD.

	Albuminous matter.	Non-nitrogenous matter.
Bare subsistence diet	100	100
Full diet with moderate exercise . .	180	147
Diet of active laborer	232	155
Diet of hard-worked laborer . . .	242	169

Thus, in passing from a bare subsistence diet to that of the hard-worked laborer, the non-nitrogenous matter of the food is less than doubled, while the albuminous matter is considerably more than doubled.

As these diet tables were adopted by various civil and military authorities as the result of experience in the practical adaptation of food to the amount of work performed, they may be regarded as expressing with great approximation to certainty the physiological requirements under different conditions. They are corroborated by the variation in diet adopted in the convict establishments of Great Britain, as given by Pavy.* In the change from "Light-labor Diet" to "Hard-labor Diet," while the non-nitrogenous food is increased only 13.37 per cent., the albuminous food is increased 16.15 per cent.

It is also a matter of interest to determine the quantity, source, and destination of the different *chemical elements* entering into the composition of the food. Taking the average composition of albuminous matters, fat, and carbohydrates, we find that a man under ordinary full diet takes into his system daily the constituents of the food, in round numbers, as follows:

DAILY CONSUMPTION IN THE FOOD.

		C	H	O	N	S
Albuminous matter,	130 grammes, containing	70	10	29	20	1
Starch . .	300 " "	134	18	148		
Fat . . .	100 " "	76	12	12		
		280	40	189		

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*On Food and Dietetics. Philadelphia edition, 1874, p. 433.

Of these elementary bodies, carbon and nitrogen are considered especially important; carbon as forming the most abundant and characteristic ingredient of all organic combinations, and nitrogen as the distinguishing element of albuminous substances. Of these two, the system requires daily, in an active condition, about 20 grammes of nitrogen and about 280 grammes of carbon. This alone makes it evident that a mixed diet of animal and vegetable food is the most available for man. Meat contains, according to Payen, 3 per cent. of nitrogen and 11 per cent. of carbon. Consequently, if the diet were composed exclusively of this food, the necessary quantity of nitrogen would be supplied by 666 grammes of meat; but in order to obtain the required carbon, 2,545 grammes would need to be consumed, thus involving a waste of its nitrogenous matter. On the other hand, bread, the most nutritious of vegetable substances, contains 1 per cent. of nitrogen and 30 per cent. of carbon. Therefore, if this were the only food used, 933 grammes would be sufficient to supply all the carbon; but, in order to obtain the due amount of nitrogen, it would be necessary to consume 2,000 grammes. A mixture, accordingly, of the two kinds of food, in which nitrogenous and hydrocarbonaceous matters respectively preponderate, is best adapted to supply the wants of the system without unnecessary expenditure of material.

The changes undergone in the body by the ingredients of the food, and their final destination, vary for different kinds. The carbohydrates no doubt, after serving their purpose in the animal economy, are finally expelled under the form of carbonic acid and water. The oxygen, introduced with the inspired air, produces this result by uniting with the carbon of the organic body, while its hydrogen and oxygen, already present in the relative quantities to produce water, are liberated under that form. This result is expressed by the following formula:

$$\underset{\text{Starch.}}{C_6H_{10}O_5} + O_{12} = \underset{\text{Carbonic acid.}}{6(CO_2)} + \underset{\text{Water.}}{5(H_2O)}.$$

Thus the change undergone by starch and allied substances in the animal body, where they are consumed, is precisely the reverse of that taking place in the act of vegetation, by which they are produced.

For the fats the change is a similar one, their only final products, so far as we know, being carbonic acid and water. But for this they require, as already mentioned, a greater supply of extraneous oxygen, since, beside their larger proportion of carbon, they also contain hydrogen which requires further oxidation, to form water. The change thus undergone by fatty substances may be expressed as follows:

$$\underset{\text{Fat.}}{C_{51}H_{98}O_6} + O_{145} = \underset{\text{Carbonic acid.}}{51(CO_2)} + \underset{\text{Water.}}{49(H_2O)}.$$

In the case of albuminous matters the process is a different one. These substances contain an element, namely, nitrogen, which does not appear in the carbonic acid and watery vapor of the expired breath, but forms a distinguishing constituent of the crystallizable matters of the urine. Of these matters, urea is by far the most abundant, and fully five-sixths of the nitrogen taken in with the food reappears as an ingredient of urea, while the remainder is included in the creatinine and uric and hippuric acids of the urine, and in the excrementitious substance of the feces.

There is evidence, however, that albuminous matters also take part in the formation of carbonic acid; that is, although all their nitrogen is discharged under the form of urea and other similar combinations in the urine and feces, all their carbon does not appear in these excretions, and must pass out by some other channel. While, as we have seen, 130 grammes of albuminous matter are taken daily with the food, containing 70 grammes of carbon, only 35 grammes of urea are discharged during the same time, containing 7 grammes of carbon; and, according to the most accurate analyses,* not more than 23 grammes are discharged daily by both the urine and feces together. This leaves unaccounted for about 47 grammes of carbon, or two-thirds of the original quantity, which must pass out from the body under some other form of combination. The same thing is true, to a considerable extent, of the hydrogen of these substances, of which 10 grammes are introduced daily with the albuminous matters of the food, while not more than 5 or 6 grammes are discharged in organic combinations with the urine and feces. The albuminous matters, therefore, not only give rise to the elimination of urea, but also contribute to the production of carbonic acid and water.

The manner in which this takes place is probably by the separation of some of the elements of albumen, in the form of urea, while the remainder are left behind as a non-nitrogenous substance. If we adopt, for the constitution of an albuminous body, exclusive of its sulphur, Lieberkühn's formula, $C_{72}H_{112}N_{18}O_{22}$, and take away from it all the nitrogen in the form of urea, a substance will remain analogous in composition to a fat, thus—

Albumen	C_{72}	H_{112}	N_{18}	O_{22}
9 Urea (CH_4N_2O)	C_9	H_{36}	N_{18}	O_9
	C_{63}	H_{76}		O_{13}

The remaining substance may then undergo complete oxidation without the further production of a nitrogenous compound. This double result of the decomposition of the albuminous substances, together with the fact that we take habitually three or four times as much non-nitrogenous as nitrogenous matter in the food, will explain the preponderance of carbonic acid as an excretion over urea. For while the average daily quantity of urea is only 35 grammes, the carbonic acid exhaled with the breath amounts to from 700 to 800 grammes; the quantity of carbonic acid produced being, by weight, fully twenty times as great as that of the urea. Urea is a nitrogenous

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* Ranke, Grundzüge der Physiologie des Menschen. Leipzig, 1872, p. 298.

substance separated by decomposition from the albuminous ingredients of the system; while carbonic acid represents its remaining carbonaceous elements in union with oxygen introduced by the breath.

The quantities of the various substances taken with the food and discharged with the excretions are liable to many variations from the changing condition of the individual. If the body be increasing in weight, the substances introduced will be more than those discharged; if it be diminishing, the material discharged will be more than that introduced. Even in the healthy adult, where the body does not sensibly gain or lose for long intervals, observation has shown that there are frequent fluctuations of small extent, and that the income for any single day rarely counterbalances exactly the outgo for the same period. Consequently the preceding tables cannot be taken as furnishing, in any case, a uniform and invariable standard, but only as showing what, on the whole, are the relative quantities of the ingredients of the food and the bodily frame. Although we are not yet able to determine all the changes which they undergo in the system, there is no doubt of the main result produced by their transformation. On the one hand, we have certain nutritious substances introduced, and, on the other, certain excrementitious products discharged, forming a double series, which may be expressed as follows:

INTRODUCED WITH THE FOOD.	DISCHARGED WITH THE EXCRETIONS.
Albuminous matter.	Urea.
Fat.	Carbonic acid.
Carbohydrates.	Water.

This represents the decomposition and metamorphosis of the organic substances proper; while the mineral ingredients of the food, as a rule, pass through the system unchanged.

SECTION II.

FUNCTIONS OF NUTRITION.

CHAPTER I.

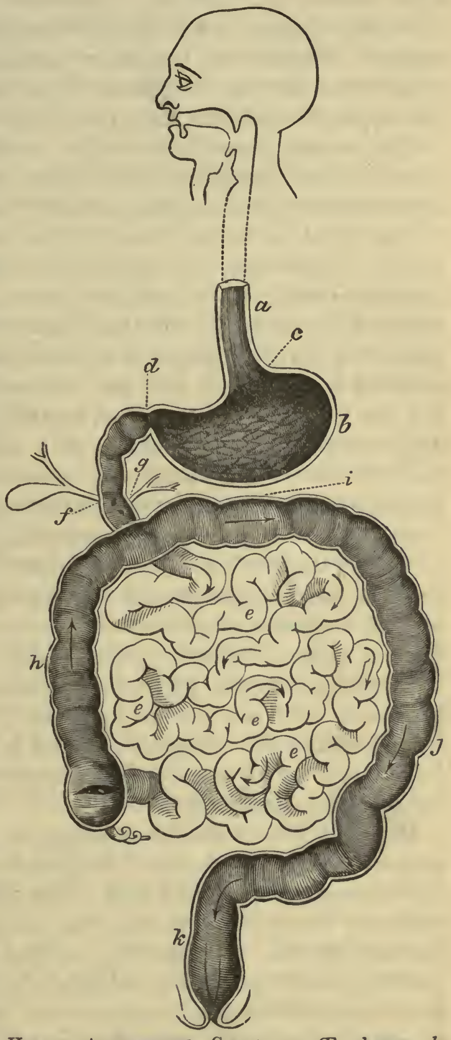
DIGESTION.

THE first act in the process of nutrition is that by which the food is liquefied and made capable of absorption. Animals and man require for their sustenance organic materials; that is, substances which have already formed part of organized bodies. When taken as food these matters are almost invariably solid or semi-solid, and insoluble in water. The alimentary constituents of meat, grain, herbage, and vegetables are mainly solid in form; and even the nutritious substances, naturally fluid, such as milk, white of egg, and other albuminous liquids, are usually more or less solidified by cooking, when used for human food. These substances, accordingly, before they can be taken up by the blood-vessels, and made available for the nourishment of the tissues, need to be reduced to a soluble condition. The preliminary act, by which this is accomplished, is the process of digestion.

While there are many variations of detail in the digestive process, according to the structure and habits of different animals, its essential features are everywhere the same. The food is taken into a canal, running through the body from mouth to anus, known as the "alimentary canal," exhibiting, at various points, enlargements, constrictions, or diverticula, and receiving the secretions of various accessory glands. While passing through this canal it comes in contact with certain digestive fluids, secreted by the mucous membrane of the canal and by the accessory glands,—which act upon it in such a way as to liquefy its ingredients, or otherwise modify their physical condition. As the alimentary mass passes from above downward, urged by the muscular action of the intestine, its liquefied parts are removed by absorption; while the remainder, consisting of the indigestible portions, with the refuse of the intestinal secretions, gradually acquires the consistency of feces, and is finally discharged under that form from the intestine.

The alimentary canal varies in different animals, according to the comparative development of its different parts. In herbivorous animals generally, it is longer and more complicated than in the carnivora. In man, where it holds an intermediate position in this respect, it is about six times the length of the body. Its principal divisions, enumerated from above downward, are: the mouth, the pharynx, the œsophagus, the stomach, the small intestine, and the large intestine. At its commencement (Fig. 20) is the cavity of the *mouth*, which communicates, immediately beyond the fauces, with the pharynx. From the pharynx, a straight tubular canal, the œsophagus (*a*), leads directly to the *stomach* (*b*), a flask-shaped expansion, surrounded at its cardiac and pyloric orifices (*c*, *d*) by special bands of muscular fibres. Then follows the *small intestine* (*e*), different parts of which, owing to certain differences in size, structure, or convolution, bear the names of duodenum, jejunum, and ileum. In the uppermost division, or duodenum, are the orifices of the biliary and pancreatic ducts (*f*, *g*). Lastly, comes the *large intestine* (*h*, *i*, *j*, *k*) separated from the preceding by the ileo-cæcal valve, and terminating at the anus, where it is provided with a double sphincter muscle guarding its orifice. Everywhere the alimentary canal is composed of a mucous membrane and a muscular coat, with a layer of connective tissue between the two. The muscular coat consists of a double layer of longitudinal and transverse fibres, by the alternate contraction and relaxation of which the food is carried through the canal from above downward. The mucous membrane presents a different structure in different parts. That of the mouth and œsophagus is smooth, with a hard, white, tessellated epithelium, which terminates abruptly at the cardiac orifice of the stomach. The mucous membrane

Fig. 20.



Human Alimentary Canal.—*a*. Œsophagus. *b*. Stomach. *c*. Cardiac orifice. *d*. Pylorus. *e*. Small intestine. *f*. Biliary duct. *g*. Pancreatic duct. *h*. Ascending colon. *i*. Transverse colon. *j*. Descending colon. *k*. Rectum.

of the gastric cavity is soft and glandular, covered with transparent, columnar epithelium, and thrown into minute folds, often reticulated with each other. In the small intestine it presents larger transverse folds, known as "valvulæ conniventes," is covered with villosities of various forms, and contains throughout an abundance of tubular follicles. Finally, in the large intestine the mucous membrane is smooth and shining, free from villosities, and provided with a glandular apparatus different from that of the preceding parts.

The accessory glandular organs of the digestive apparatus are the salivary glands communicating with the cavity of the mouth, and the liver and the pancreas connected with the duodenum.

The *digestive fluids*, derived from these sources, are five in number; namely, 1st, the saliva secreted by the salivary glands, and discharged into the mouth; 2d, the gastric juice, supplied by the mucous membrane of the stomach; 3d, the pancreatic juice, produced by the pancreas, and conveyed through its duct into the duodenum; 4th, the bile supplied by the liver, and also discharged into the duodenum; and, 5th, the intestinal juice secreted by the glandules of the small intestine. These fluids have, in general, certain well marked characters, by which they are readily distinguished from each other, and which indicate corresponding differences in their physiological properties. At the same time each one is a compound secretion, containing various organic ingredients, the product of different physiological acts. Thus the three pairs of salivary glands and the buccal follicles unite their secretions to form the saliva of the mouth; the gastric juice contains an organic ferment and a free acid, both essential to its physiological activity, and produced in the stomach by dissimilar secretory operations; the pancreatic juice contains no less than three different albumenoid matters; and the bile is equally complex in the number and quality of its ingredients. This is a general feature of the secretions belonging to the digestive apparatus.

It is the aim of the physiologist to ascertain the constitution and properties of each digestive fluid, and to learn, if possible, its action on the ingredients of the food. For this purpose, the method of experiment by artificial fistulæ has been largely used, and with very valuable results. By inserting a silver canula into the parotid or submaxillary duct, in various animals, the secretion of either gland may be obtained without admixture from other sources. A fistula of the stomach, established through the abdominal walls, supplies us with gastric juice, and similar methods have been adopted with the gallbladder and the pancreatic duct. By this means the time, rapidity, and quantity of each secretion is ascertained, as well as its variations under external or internal influences. The digestive fluids of different animals are compared with each other, and with those obtained by accidental fistulæ in man. Lastly, the secretions are placed in contact with different alimentary substances, in flasks or test tubes, at the temperature of the body, and their action investigated by the mode of artificial digestion. It appears from these experiments, in general terms, that each digestive fluid has not only an action of its own, but that each one of its ingredients contributes in a special way to the digestive process.

Beside the use of artificial fistulæ there is still another method for the experimental study of the digestive fluids. It is based on the fact that the principal organic ingredient of a secretion is in most instances produced in the solid substance of the gland, and may be extracted by proper solvents from its tissue. To the solution thus obtained, the needed accessory ingredients, such as saline matters, or dilute acids or alkalies, are added, and an artificial digestive fluid thus produced, similar in most respects to the natural one. It is then subjected to examination in regard to its influence on alimentary substances. This method has received a wide extension of late years with the use of glycerine as a convenient menstruum for the extraction of glandular products. It has been the source of much important information, but its results need to be verified, in every instance, by examination of the normal secretion in the living animal.

The digestive fluids and their mode of action are especially characterized by the presence of *ferments.* In every instance where their digestive function is plainly evident, its dependence on the activity of a ferment is equally unmistakable. In experimental digestions, with either the normal secretion, or artificial extracts, all the conditions of moisture, temperature, degree of concentration, and the like, requisite for the operation of organic ferments, must be maintained; and when such an experiment is successfully carried out, the quantity of alimentary material digested is far greater than that of the organic ingredient which produces the effect.

The *nature of the change* caused by digestion in the alimentary substances is partly physical and partly chemical. But although this change is indispensable for the absorption of these substances in due quantity, it does not consist in any profound alteration of their chemical characters. The alimentary materials are not decomposed, nor converted into substances of a different kind. They are simply transformed into soluble materials of the same class with themselves. The carbohydrates after digestion remain carbohydrates, the albumenoid matters are still albumenoids, and the fatty substances retain the chemical properties of the fats. The transformation of starch into glucose by the digestive process is an act of hydration, which may be accomplished by continued boiling with water and a mineral acid outside the body. Albuminous matters, in digestion, are converted into peptones. This change is also regarded as a hydration, and it has further been shown that albumen may be made to undergo a similar transformation by long boiling in acidulated water, or by boiling at a high temperature under pressure. Thus the animal ferments, in the alimentary canal, act by inducing rapidly, at the temperature of the body, changes which would otherwise require a longer time or more powerful agencies. Lastly, the fatty substances are reduced to a state of emulsion, and in this condition diffused through the digestive fluids. This effect, which is mainly due to the contact of an albuminous liquid, may be aided by a partial acidification and saponification; but the principal mass of the fat, in undergoing the digestive process, only assumes the form of a chylous emulsion. All the alimentary substances are accordingly made ready for absorption, without losing the essential features of their chemical constitution.

In the following pages the properties of the digestive fluids will be considered in detail, together with the action exerted upon the food in different parts of the alimentary canal.

Mastication.

The process of mastication, which takes place in the mouth, consists of a mechanical trituration of the food by the teeth. At the same time it is mingled with the saliva, which is so worked into the alimentary mass as to reduce it to a pasty condition. By this means the solid substances of the food, finely divided and thoroughly moistened, are rendered susceptible to the action of the digestive fluids. Food swallowed either in large masses or in a dry condition would be slowly affected by the alimentary secretions, and would be consequently difficult of digestion; but, when comminuted and softened by mastication, it presents a large surface of contact and a ready permeability, favorable to the prompt action of the digestive solvents.

The form of the teeth and their physical action vary in different animals according to the nature of their food; being adapted, in the carnivora, mainly for wounding and lacerating; in the rodentia for gnawing and cutting, and for grinding in the herbivora. In man they are adapted for a mixed diet of animal and vegetable food, and combine a general resemblance to each other, with certain special characters in different parts of the mouth. The incisors, four in number, in each jaw, are more or less chisel-shaped, with a cutting-edge running from side to side. They are useful in separating from a mass of food the proper quantity to be taken into the mouth. The canine teeth, one on each side, in each jaw, placed immediately behind the former, are somewhat pointed in form, and are immediately followed by the two anterior molars, which are thicker and stronger. Finally, the three posterior molars, on each side of each jaw, complete the dental arch posteriorly. They are the largest and strongest of the set, firmly planted in the jaw, and present upon their free extremity a number of conical and ridge-like elevations, separated by shallow furrows. They are especially adapted, by their form, size, and situation, for the comminution of resisting substances, and they perform, with the anterior molars, the main part of the work of mastication. The enamel which covers the crowns of all the teeth, and which is the hardest substance in the body, protects their substance from injury, and enables them to exert the necessary physical action upon the food.

Notwithstanding the simple character of the masticatory act, it is one of great practical importance. If hurriedly or imperfectly performed, it leaves the food in a crude and intractable condition, liable to cause subsequent disturbance in the digestive process. It is a necessary preliminary for the more complicated physiological changes to take place in the remainder of the alimentary canal.

Saliva.

The saliva is a compound fluid, derived from the secretion of four different glandular organs—namely, the parotid, submaxillary, and sublingual glands, and the muciparous glandules of the mouth. The glands have a general resemblance to each other in structure, being composed of distinct irregularly ovoidal masses, more or less flattened into a polygonal form by mutual compression. These masses or *lobules* are connected with corresponding branches of the salivary duct, which penetrate into their interior, and there divide into smaller tubes, each one of which terminates in a rounded sac called the *glandular follicle* or alveolus. The appearance presented upon an injection of such a lobule is as if the follicles were arranged in clusters, like grapes, around the ends of the smaller salivary tubes. (Fig. 21.) A more complete examination has shown, however, that the follicles are simply the rounded extremities of tubular or sac-like offshoots from the salivary tube; and that it is the windings and prolongations of the tube which constitutes the secreting follicles of the gland. The follicles are in general about 50 mmm. in diameter, and are lined with *glandular epithelium cells*, which cover their internal surface and nearly fill their cavity; so that there is often only a small space, toward the central part of the follicle, containing a transparent fluid produced by the secreting action of the cells. The cells, which are arranged in a single layer, are finely granular bodies, about 15 mmm. in diameter, each with an oval nucleus, situated toward the external part of the follicle. They are closely packed together in various polygonal forms.

Fig. 21.

Lobule of Parotid Gland of newly-born infant, injected with mercury. (Wagner.)

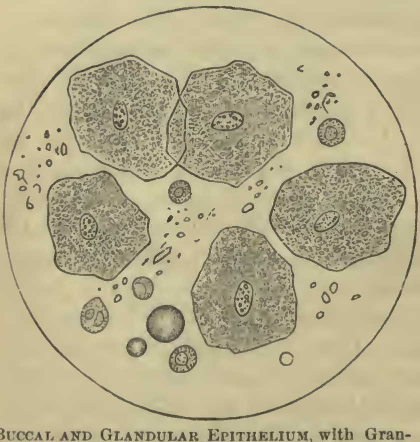
The *salivary tubes* or *ducts*, outside the follicles, unite into larger branches, until they reach the principal excretory duct. They are lined with cells which differ in form from those of the follicles, being elongated and cylindrical, each with a nucleus situated about its middle portion. It is probable that the epithelium of the salivary ducts, as well as that of the follicles, takes part in the process of secretion; since Pflüger has found that in sections of the gland, examined immediately after being taken out of the body, drops of transparent fluid may be seen exuding from the ends of the cylindrical epithelium cells into the cavity of the duct. The follicles and lobules are surrounded with a delicate layer of connective tissue, in which are distributed the capillary blood-vessels, supplying the materials for secretion.

Fig. 22.

Section of the Submaxillary Gland from the Dog.—*a.* Salivary duct, with cylindrical epithelium and central cavity. *b.* Follicle, with glandular epithelium and central cavity. (Kölliker.)

Physical Properties and Composition of the Saliva.—Human saliva, from the cavity of the mouth, is a colorless, slightly viscid, alkaline fluid, with a specific gravity of 1.005. When first discharged, it is frothy and opaline, holding in suspension minute flocculi. After standing for some hours in a cylindrical vessel, an opaque, whitish deposit collects at the bottom, while the supernatant fluid becomes clear. This deposit (Fig. 23), consists of epithelium scales from the internal surface of the mouth, detached by mechanical attrition, minute, roundish, granular, nucleated cells, apparently epithelium from the mucous follicles, some granular matter, and a few oil-globules. The supernatant fluid has a faint bluish tinge, and becomes slightly opalescent by boiling or by the addition of nitric acid. Alcohol in excess causes the precipitation of abundant whitish flocculi.

Fig. 23.



Buccal and Glandular Epithelium, with Granular Matter and Oil-globules; deposited as sediment from human saliva.

According to the analyses of Bidder and Schmidt, the composition of saliva is as follows:

Composition of the Saliva.

Water	995.16
Albuminous matter	1.34
Potassium Sulphocyanide	0.06
Calcareous, magnesian, and alkaline phosphates	0.98
Sodium and Potassium chlorides	0.84
Mixture of epithelium	1.62
	1000.00

Saliva, accordingly, is one of the least concentrated of the digestive secretions, containing but a small quantity of organic matter, and by no means a large proportion of mineral salts; its watery ingredient being by far the most abundant, as compared with the other animal fluids. Its albuminous matter consists of a small quantity of *albumen*, coagulable by heat or a mineral acid; more or less *mucine*, which gives to it a slightly viscid character, and is coagulable by acetic acid; and *ptyaline*, a substance belonging to the class of ferments, which is thrown down by alcohol in excess. Some of these reagents, accordingly, precipitate all the albuminous matters present, while others coagulate only a part of them. The sulphocyanide may be detected by adding to the saliva a small quantity of a solution of iron chloride, when the characteristic red color of iron sulphocyanide is produced. A similar red color is produced by the action of the ferric salts upon *meconic acid*, or the meconates; but the two may be distinguished from each other by the fact that the red color caused by the presence of a sulphocyanide is destroyed by the addition of either gold chloride or mercurial bichloride, neither of which affects that produced by meconic acid. The presence of a sulphocyanide in human saliva is almost constant, and we have never failed to find it in the freshly collected secretion. Vierordt has calculated its amount in saliva by measuring the absorption of light in the green and blue portions of the spectrum of the red fluid produced on the addition of iron chloride; and has found it, in an average of six observations, to be 0.16 parts per thousand.

Saliva, like various other animal fluids, has the property of converting boiled starch into glucose at the temperature of 38° C. Its action is not strictly confined to this temperature, but will go on, though with diminished rapidity, both above and below it, if the variation be not too great. It is suspended, however, at or near the freezing-point, and is permanently arrested by boiling water. It depends on the presence of ptyaline, the special ferment of the saliva, which, like other similar bodies, is most active at or near the temperature of the living body. It is differently affected, however, by cold and heat. By a freezing temperature its action is suspended for the time, but recommences when warmth is again applied; while boiling permanently destroys its catalytic property.

The secretions produced by the different salivary glands vary in their physical properties, especially in the degree of their viscidity.

The *parotid saliva* may be obtained, from the human subject, in a state of purity, by introducing into the orifice of Steno's duct, through the mouth, a silver canula, about one millimetre in diameter. The other extremity of the canula projects between the lips, and the saliva is collected from its orifice.

The result of many observations, conducted in this manner, is that human parotid saliva is colorless, watery, and alkaline in reaction. It differs from the mixed saliva of the mouth, in being perfectly clear, without turbidity or opalescence. Its flow is scanty while the jaws remain at rest; but if the movements of mastication are excited by the introduction of food, it runs in much greater abundance. We have collected, in this way, from the parotid ducts of one side only, in a healthy man, 31.1 grammes of saliva in twenty minutes; and in seven successive observations, made on different days, comprising in all three hours and nine minutes, we have collected a little over 194 grammes.

Parotid saliva may be obtained from the dog by exposing Steno's duct where it crosses the masseter muscle, and introducing into it, through an artificial opening, a silver canula. The secretion then runs from the external orifice of the canula, without being mixed with the other salivary fluids. It is clear, limpid, and watery, and without perceptible viscidity, resembling in these respects the parotid saliva of man. The *submaxillary* saliva of the dog is obtained in a similar manner, by inserting a canula into Wharton's duct. It differs from the parotid secretion, as regards its physical properties, chiefly in possessing a well marked viscidity. The *sublingual* saliva is also colorless and transparent, and is more viscid than that from the submaxillary. The secretion of the muciparous glandules has been obtained by placing a ligature simultaneously on Wharton's and Steno's ducts, and on that of the sublingual gland, so as to shut out from the mouth all their secretions, and then collecting the fluid supplied by the mucous membrane. This fluid is very scanty, and so much more viscid than the other secretions that it adheres strongly to the surface of a glass vessel. All the salivary secretions of the dog are alkaline in reaction. They differ from those of man chiefly in the absence of ptyaline, and in their consequent want of action on starchy substances.

Mode of Secretion of the Saliva. — The salivary glands differ from each other in the abundance of their secretion and in the influences which excite their activity. The parotid saliva is most abundantly poured out under any stimulus which excites the movement of the jaws, such as the mastication of dry substances, or continuous speaking. According to Bernard, the submaxillary secretion is especially increased by the introduction of substances which excite the taste; while that of the sublingual glands in the dog is exuded at the moment of deglutition, and aids, with that of the muciparous glandules, in lubricating the mouth and fauces, and facilitating the passage of the food. Colin,* in experimenting upon the horse and the ox, also found the parotid saliva excited by the movements of mastication, while the submaxillary secretion was increased by introducing into the mouth substances having a marked taste. Both the parotid and submaxillary secretions are abundant while the animal is feeding, their quantity being proportional to the rapidity of mastication and the sapid quality of the alimentary substances. They are both either suspended or much diminished during abstinence. In the ruminants, the sublingual saliva, like the submaxillary, is excited by sapid substances and while the animal is feeding. Its secretion continues during abstinence, contributing to keep the surfaces in a moist condition.

Another indication of the different nervous influences by which the salivary glands are controlled, is that in the ruminant animals, while feeding, both the parotid and submaxillary glands furnish an abundant supply of saliva; but during rumination, although the parotid glands are in full secretion, discharging frequently as much as 900 grammes in fifteen minutes, the submaxillary glands are nearly or quite inactive. Colin has also found that in the ox, horse, and ass, the parotid glands of the two opposite sides, during mastication, are never in active secretion at the same time; but that they alternate with each other, one remaining quiescent while the other is active. In these cases mastication is said to be *unilateral;* that is, when the animal begins feeding or ruminating, the food is triturated for fifteen minutes or more by the molars of one side only. It is then changed to the opposite side, where mastication is performed for the succeeding fifteen minutes. It is then changed back again, and so on alternately; the direction of the lateral movements of the jaw being frequently reversed during the course of a meal. By establishing a salivary fistula simultaneously on each side, it is found that the flow of saliva corresponds with the direction of the masticatory movement. When the animal masticates on the right side, it is the right parotid which secretes actively, while but little is supplied by the left; when mastication is on the left side, the left parotid pours out an abundance of fluid, while the right is nearly inactive.

We have observed a similar alternation in the human subject, when mastication is changed from side to side. In an experiment of this kind, the canula being inserted into the parotid duct of the left side, the quantity of saliva discharged during twenty minutes, while mastication was performed mainly on the opposite side of the mouth, was 8.26 grammes; while the quantity during the same period, mastication being on the same side of the mouth, was 24.25 grammes. It was therefore nearly three times as much in the latter case as in the former.

Daily Quantity of the Saliva.—Owing to variations in the rapidity of secretion of the saliva, and also to the fact that it is not excited in the same way by artificial stimulus as by the presence of food, it is

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* Physiologie comparée des Animaux Domestiques. Paris, 1854, tome i., p. 468.

somewhat difficult to ascertain with exactness its total daily quantity. The first attempts to do so were made upon patients affected with parotid fistula, and the amounts collected were so small as to lead to the conclusion that the entire quantity of saliva was not more than ten or twelve ounces, or about 350 grammes per day. Bidder and Schmidt,* from more extended observation, were led to make a higher estimate. One of these observers, in experimenting upon himself, collected from the mouth in one hour, without artificial stimulus, 97 grammes of saliva; and he calculates the amount secreted daily, making an allowance of seven hours for sleep, as not far from 1620 grammes.

On repeating this experiment we have not been able to collect from the mouth, without artificial stimulus, more than 36 grammes of saliva per hour. This quantity, however, may be greatly increased by introducing into the mouth any smooth unirritating substance, such as glass beads or the like; and during the mastication of food, the saliva is poured out in much greater abundance. Even the sight or odor of nutritious food, when the appetite is excited, will stimulate to a remarkable degree the flow of saliva. Any estimate, therefore, of its total quantity, based on the amount secreted in the intervals of mastication, would be imperfect. We may make a tolerably accurate calculation by ascertaining how much is really secreted during a meal, over and above that which is produced at other times. We have found, by experiments performed for this purpose, that wheaten bread gains during complete mastication 55 per cent. of its weight of saliva; and that fresh cooked meat gains, under the same circumstances, 48 per cent. of its weight. We have already seen that the daily allowance of these two substances, for a man in full health and activity, is about 540 grammes of bread and 450 grammes of meat. The quantity of saliva, accordingly, employed in mastication is, for the bread 297 grammes, and for the meat 216 grammes, making in all 513 grammes. According to the observations of Tuczek,† which were made in a similar manner on different individuals, the average daily requirement is somewhat less, namely, 469 grammes. If we accept the mean of these two results, and calculate the quantity secreted between meals as continuing for twenty-two hours at the rate of 36 grammes per hour, we have:

Saliva required for mastication	=	491	grammes.
" secreted in intervals of meals	=	792	"
Total quantity per day, a little over		1280	"

Physiological Action of the Saliva.—The principal function of the saliva is undoubtedly to moisten the food and provide in this way for its further solution, and especially to assist in mastication, by which the food is converted into a pultaceous mass. This is mainly accomplished by the watery ingredients of the secretion, while the albuminous

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* Verdauungssaefte und Stoffwechsel. Leipzig, 1852, p. 1.

† Zeitschrift für Biologie. München, 1876, Band xii., p. 534.

matters aid in giving to the masticated food the requisite consistency, and also serve to lubricate its surface and facilitate deglutition. This is evident from the fact that the principal trouble resulting from deficiency of the saliva is a difficulty in the mechanical processes of mastication and swallowing. Food which is hard and dry, like crusts or crackers, cannot be masticated and swallowed with readiness, unless properly moistened. If the saliva be excluded from the mouth, its loss does not interfere so much with the chemical changes of the food in digestion, as with its physical preparation. This is the result of experiments performed by various observers. Bidder and Schmidt,* after tying Steno's duct, together with the common duct of the submaxillary and sublingual glands on both sides in the dog, found that the immediate effect of such an operation was "a remarkable diminution of the fluids exuding upon the surfaces of the mouth; so that these surfaces retained their natural moisture only so long as the mouth was closed, and readily became dry on exposure to the air. Deglutition was therefore rendered difficult not only for dry food, like bread, but even for that of a tolerably moist consistency, like fresh meat. The animals also became very thirsty, and were constantly ready to drink."

Bernard† also found that the only marked effect of cutting off the flow of saliva was a difficulty in mastication and deglutition. He first administered to a horse 500 grammes of oats, and found that this quantity was masticated and swallowed in nine minutes. An opening had been previously made in the œsophagus at the lower part of the neck, so that none of the food reached the stomach; each mouthful, as it passed down the œsophagus, being received at the opening and examined by the experimenter. The parotid duct on each side of the face was then divided, and another similar quantity of oats given to the animal. Mastication and deglutition were at once retarded. The alimentary masses passed down the œsophagus at longer intervals, and their interior was no longer moist and pasty, but dry and brittle. Finally, at the end of twenty-five minutes, the animal had succeeded in masticating and swallowing only about three-quarters of the quantity which he had previously disposed of in nine minutes.

It appears, furthermore, from the experiments of Magendie, Bernard, and Lassaigne, on horses and cows, that the quantity of saliva absorbed by food during mastication is in direct proportion to its hardness and dryness, but has no particular relation to its chemical qualities. These experiments were performed as follows: The œsophagus was opened at the lower part of the neck, and tied between the wound and the stomach. The animal was then supplied with a previously weighed quantity of food, and this, as it passed out by the œsophageal opening, was collected and again weighed. The difference in its weight, before and after swallowing, indicated the quantity

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* Verdauungssaefte und Stoffwechsel, p. 3.

† Leçons de Physiologie Expérimentale. Paris, 1856, p. 146.

of saliva absorbed. The following table gives the results of some of Lassaigne's experiments upon a horse:

Kind of Food employed.		Quantity of Saliva absorbed.
For 100 parts of	hay	400 parts.
"	barley meal	186 "
"	oats	113 "
"	green stalks and leaves	49 "

It is evident from the above that the quantity of saliva used in mastication has not so much to do with the chemical character of the food as with its physical condition. When the food is dry and hard, it requires much mastication and the saliva is secreted in abundance; when it is soft and moist, a smaller quantity of the secretion is poured out; and finally, food taken in a fluid form, as soup or milk, or reduced to powder and moistened with a large quantity of water, is not mixed at all with saliva, but passes at once into the stomach.

The action of human saliva which converts boiled starch into sugar, would seem to indicate a further connection with the digestive process. This action will sometimes take place with great promptness in an artificial mixture of starch and saliva. Traces of glucose may be detected in such a mixture in one minute after the two substances have been brought in contact; and starch paste, introduced into the mouth, if already at the temperature of 38° C., will yield traces of sugar at the end of half a minute. Its rapidity, nevertheless, as noticed by Lehmann, varies much at different times. It is frequently impossible, even with the mixture kept steadily at the temperature of 38° C., to find evidence of sugar under five, ten, or fifteen minutes; a difference probably dependent on the varying constitution of the saliva.

Notwithstanding, furthermore, the occasional rapidity of this action, it is not, on the whole, a very efficient one in regard to quantity; that is, only a small portion of the starch is converted into glucose within a given time, the greater part remaining unchanged. This is proved by the fact that such a mixture will exhibit the reaction of starch with iodine long after Fehling's test has shown the existence of glucose. If a solution of boiled starch, in the proportion of 3 parts of starch to 100 parts of water, be mixed with one-third its volume of fresh human saliva, and placed in the water-bath at the temperature of 38° C., it will often give, in one minute, a prompt sugar-reaction with Fehling's test; but it also contains, at the same time, an abundance of unaltered starch. Even at the end of an hour, according to our own observations, the starch is far from being entirely converted, and the mixture will still give a strong purple-blue color on the addition of iodine. The same persistence of starch in considerable proportion may be seen when the mixture is retained in the mouth. If a thin paste of boiled starch, containing no traces of sugar, be taken into the mouth and thoroughly mixed with the buccal secretions, it will often, as above mentioned, begin to show the reaction of glucose in half a minute;

but some of the starchy matter still remains, and will continue to manifest its reaction with iodine for fifteen or twenty minutes, or even for half an hour.

These facts have an evident bearing on the disputed question whether the sugar-producing property of human saliva be an essential part of its physiological action; that is, whether the saliva, in fact, transforms the starch of the food into glucose. If the digestion of the food took place in the mouth, or if it were retained there for any considerable time, there would be no doubt in this respect. But in reality the passage of the food through the mouth is momentary, and only sufficient for mastication. This time is too short for complete conversion of the abundant starchy matter in bread or vegetables, which must be swallowed into the stomach in great measure still unchanged. Some observers (Schiff, F. G. Smith, Flint, Ranke, Brunton) believe that the transforming action of the saliva, commenced in the mouth, may continue in the stomach in presence of the gastric juice. Others (Bernard, Robin, Colin) assert that the action of the saliva on starch is arrested by the gastric juice, and, consequently, does not go on in the stomach. This discrepancy, no doubt, depends partly on different modes of experimentation; some writers contenting themselves with testing the effect of dilute acids on the saliva, others using the gastric juice itself. The proportion in which the two secretions are mingled also makes a difference in the result. Our own observations lead to the conclusion that gastric juice certainly interferes with the transforming action of saliva, usually to a very marked degree, when mingled with it in equal volumes. If we take fresh unfiltered human saliva, shown by preliminary experiment to be capable of producing a prompt sugar-reaction in a solution of boiled starch at the end of one minute, mix it with an equal volume of freshly collected gastric juice from the dog, then add the starch-solution, and place the mixture in the water-bath at a temperature of 38° C., there is no sugar-reaction whatever at the end of five minutes, and only an imperfect one in half an hour; while at the end of an hour there may be distinct reduction by Fehling's test.* But if three volumes of gastric juice be added for each volume of saliva, the mixture gives no indication of sugar even at the end of an hour. It is certain that the gastric juice is secreted normally in much larger quantity than the saliva, and these proportions must be unfavorable to the continuance of starch digestion in the stomach.

All observers agree that saliva is without action on raw starch, which may remain unchanged in contact with it, at the temperature of the body, for an indefinite time. But in the herbivorous animals, whose food contains an abundance of raw starch, the salivary glands are fully developed, and saliva is secreted in large quantity. In these

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* In these examinations the fluid mixture is always treated with animal charcoal previously to applying Fehling's test; otherwise the albuminous matters of the secretions would interfere with its certainty.

animals the non-digestion of starch by saliva has been experimentally demonstrated. Colin* found the farinaceous matter of oats and starchy roots recognizable by its iodine reaction, after remaining in the first stomach of the ox, mixed with saliva, for twenty-four hours; and the same observer introduced into the interior of the paunch, through a fistula, muslin bags containing uncooked potato starch, which were found in the same cavity, still full of unaltered starch, at the end of twenty and twenty-two hours. In all cases, furthermore, the saccharine transformation of starch, as we shall hereafter see, is accomplished with great energy and promptitude by other secretions in the small intestine.

It seems evident, therefore, that the sugar-producing quality of the saliva is not a prominent part of its physiological action; but that it is mainly useful, by its physical properties, in facilitating mastication and deglutition.

It is also subservient, in an indirect way, to the nervous influences concerned in mastication. This process is aided and controlled in great measure by the sensibilities of touch and taste, in the tongue and other parts of the mucous membrane. The taste notifies us of the alimentary character of the food taken into the mouth, and its sapid qualities must be fully brought out before mastication is complete. Taste depends, for one of its essential conditions, on a sufficient supply of saliva, since no substance can produce an impression on the gustatory nerves unless it be fluid and capable of absorption. The saliva produces this effect on the soluble ingredients of the food, such as saccharine substances, saline matters, acids, or alkalies, and brings them in contact with the papillæ of the tongue in sufficient quantity to produce a gustatory sensation.

The general sensibility of the tongue enables this organ to appreciate the physical condition of the food, and its readiness for deglutition. At the same time its muscular apparatus provides for its movement in every direction. When the alimentary material is finally reduced, by the saliva and mastication, to a pasty and homogeneous condition, the softened mass is collected from every part of the mouth by the movements of the tongue, brought together upon its upper surface, and then pressed backward through the fauces into the pharynx and œsophagus. Here it passes beyond the control of the will. It is then grasped by the muscular fibres of the œsophagus, and by a continuous and rapid peristaltic action is carried downward into the stomach.

Gastric Juice.

The stomach is no doubt the organ in which the most important part of the digestive process is inaugurated, and which contributes most largely to the chemical modification of the food. Its special secretion

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* Physiologie comparée des Animaux Domestiques. Paris, 1854, tome i., p. 603.

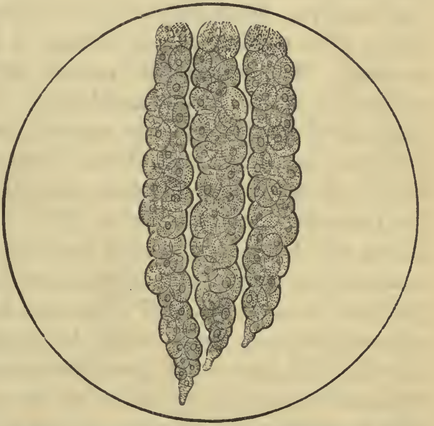
is the *gastric juice*, produced by the glandular follicles of its mucous membrane.

The mucous membrane of the stomach is soft and vascular, about one-half a millimetre thick in the cardiac portion, thence increasing in thickness to one millimetre in the middle and two millimetres in the pyloric portion. It presents an abundance of ridges or prominences about one-tenth of a millimetre in height, which in the cardiac portion are reticulated with each other, in the pyloric portion more isolated and villus-like in form. Its free surface is covered with cylindrical epithelium.

Its substance consists mainly of *tubular follicles*, lined with glandular epithelium, closely packed side by side, their bases resting upon the submucous layer, and their orifices opening upon its free surface. The space between them is occupied by the capillary blood-vessels and lymphatics, the terminal nerve fibres, and a slight framework of connective tissue. The gastric mucous membrane has therefore the character of a gland spread out in the membranous form, and surrounding the sac-like cavity of the organ.

The epithelium cells lining the follicles are of two kinds. The most abundant are pale, finely granular cells, about 13 mmm. in diameter, nearly or quite filling the cavity of the follicle in its middle and lower portions. The cells of the other variety are fewer in number, of larger size, measuring about 22 mmm. in diameter, with a distinct rounded form, often projecting from the mass of smaller cells, and causing varicose-like prominences of the contour of the follicle (Fig. 24). These cells are found in both the fundus and middle portion of the stomach, especially in its middle portion; but they do not exist in the follicles of the pyloric region, which contain cells of the smaller variety alone. In preparations stained with carmine, if taken from the stomach during the intervals of digestion, the smaller cells are tinged but slightly or not at all, while those of the larger variety exhibit a strong pinkish hue, showing a difference in their organic substance. But in specimens taken while digestion is going on, all the cells are turgid and granular, and the smaller ones not only increased in size but so altered in constitution as to be stained by the carmine solution. In preparations from the fasting animal, accordingly, the difference between the

Fig. 24.



Gastric Follicles, with large glandular cells; from middle portion of Pig's Stomach.

two kinds of cells is readily visible; while in those taken during digestion, they are hardly to be distinguished from each other.*

It is doubtful therefore whether we can infer any radical difference in function for different regions of the stomach from the form of their glandular cells. In the follicles of the middle and cardiac portions the two kinds of cells are associated, while only the smaller kind are found near the pylorus. But Ebstein† has shown that if two digestive fluids be prepared by macerating the gastric mucous membrane in acidulated water, using for one the middle portion and for the other the pyloric portion, both fluids possess digestive properties which differ only in degree. According to a still more decisive observation by Heidenhain,‡ the pyloric portion, when separated by preliminary operation from the remainder of the stomach, will yield a secretion which communicates digestive qualities to an acidulated solution. The characteristic ingredient of the gastric secretion seems to be produced more or less abundantly in all regions of the stomach, while the differences in function of its different parts, so far as they exist, relate to other particulars not yet fully understood.

The most important early observations in regard to the gastric juice, were those of Beaumont,§ in the case of Alexis St. Martin, a patient with permanent gastric fistula, the result of a gunshot wound. The wound caused an opening at the lower part of the left chest, extending through the diaphragm into the fundus of the stomach. After cicatrization of the edges of the wound, there remained a fistulous opening, about two centimetres in diameter, leading into the cavity of the stomach. The orifice was usually closed from within by a valvular protrusion of the mucous membrane; but this could be easily depressed, allowing the interior of the stomach to be inspected, or its contents to be withdrawn for examination. Beaumont's experiments, which were continued at various intervals from the year 1825 to 1832, established the following important facts: First, that the active agent in digestion is an acid fluid, secreted by the walls of the stomach; secondly, that this fluid is poured out only during digestion, under the influence of food, or of some artificial stimulus; and finally, that it will exert its solvent action on food outside the body, if kept at the temperature of 38° C. He also made investigations as to the effect of various kinds of stimulus on the secretion of the gastric juice, the rapidity with which digestion takes place, and the digestibility of various kinds of food.

The same person, with his gastric fistula unchanged, after an interval of twenty-four years, came under the observation of Prof. F. G. Smith, of the University of Pennsylvania, who again made a series of similar experiments, confirming and extending those of Beaumont. Another

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* Ewald. Die Lehre von der Verdauung. Berlin, 1879, p. 39.

† Archiv. für Mikroscopische Anatomie. Bonn, 1870, Band vi., p. 515.

‡ Archiv. für die gesammte Physiologie. Bonn, 1878, Band xviii., p. 169.

§ Experiments and Observations upon the Gastric Juice. Boston, 1834.

instance of gastric fistula, in an otherwise healthy woman, the result of local inflammation and abscess, occurred in Germany in 1854, and was investigated by Schmidt.* A third case, in some respects the most remarkable of all, happened in France in 1876. The operation of gastrotomy was performed by Verneuil, upon a young man, for impassable stricture of the œsophagus. The patient recovered with a permanent gastric fistula, through which nourishment was successfully administered. The following year the case was employed by Richet † for observations on the gastric juice.

Since 1840, similar investigations have been largely carried on by the aid of fistulæ artificially produced in various animals, the dog being most frequently employed for this purpose. These experiments have shown that the ingredients of the gastric juice, as well as its mode of action, are essentially the same in the carnivorous and herbivorous animals, and in man. The best mode of establishing a gastric fistula in the dog is as follows: A longitudinal incision, about six centimetres long, is made through the abdominal walls in the median line, over the great curvature of the stomach. The stomach is then seized with hooked forceps, drawn out at the wound, and opened with the point of a bistoury. A short silver canula, about three centimetres long and one centimetre in diameter, with a narrow flange at each end, is inserted into the wound in the stomach, the edges of which are fastened around it with a ligature, in such a way as to prevent the escape of the gastric fluids. The stomach is then returned to its place in the abdomen, the external flange of the canula resting upon the abdominal integuments, the edges of the wound being drawn together by sutures. In a few days the ligatures come away, the wounded surfaces unite, and the canula is retained in a permanent fistula; its flaring extremities preventing it from falling either out of the abdomen or into the stomach. It is closed externally by a cork, which may be removed at pleasure, allowing the contents of the stomach to be withdrawn for examination.

Mode of Secretion of the Gastric Juice.—As a rule, the gastric juice is not a constant but an occasional secretion, being poured out only when food is taken into the stomach. Beaumont found it entirely absent during the intervals of digestion, the stomach containing at that time only a little neutral or alkaline mucus. He could obtain a small quantity by gently irritating the mucous membrane with a gum-elastic catheter, or a glass rod; but on the introduction of food the mucous membrane became turgid and reddened, a clear acid fluid collected in drops beneath the mucus lining the walls of the stomach, and was soon poured out abundantly into its cavity. Prof. F. G. Smith, in his subsequent observations on Alexis St. Martin, also found the fluids obtained from the empty stomach invariably neutral in reaction; while during digestion they were always acid. Other observers, in experimenting on the dog, have found more or less acid reaction always present at the

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* Annalen der Chemie und Pharmacie. Heidelberg, 1854, p. 42.

† Comptes Rendus de l'Académie des Sciences. Paris, 1877, tome lxxxiv., p. 450.

surface of the mucous membrane. According to our own observations, the irritability of the gastric mucous membrane, and the readiness with which the flow of gastric juice may be excited, varies considerably in different animals of the same species. In dogs, we have found in one instance that the gastric juice was always entirely absent in the intervals of digestion; the mucous membrane presenting either a neutral or slightly alkaline reaction. In this animal, which was perfectly healthy, the secretion could not be excited by any artificial means, such as glass rods, metallic catheters, or the like; but only by the stimulus of ingested food. Indigestible pieces of tendon, introduced through the fistula, were expelled in a few minutes, without exciting the flow of a single drop of acid fluid; while pieces of fresh meat, introduced in the same way, produced at once an abundant supply. In other instances the introduction of metallic catheters or glass rods into the empty stomach has produced a scanty flow of gastric juice; and in dogs killed by section of the medulla oblongata, we have usually, though not always, found the gastric mucous membrane with a distinctly acid reaction, even after an abstinence of six, seven, or eight days. Under these circumstances there is never any considerable amount of fluid in the stomach; but only enough to moisten the mucous membrane, and give it an acid reaction.

The gastric juice obtained by irritating the stomach with a metallic catheter is not sufficient in quantity for extended experiments. For that purpose, the animal should be fed, after a fast of twenty-four hours, with fresh lean meat, slightly hardened by short boiling, in order to coagulate the fluids of the muscular tissue, and prevent their mixing with the gastric secretion. Usually no effect is apparent within five minutes after the introduction of food. At the end of that time the gastric juice begins to flow slowly and in drops. It is at first colorless, but soon acquires a slight amber tinge. It then runs more freely, usually in drops, but often for a few seconds in a continuous stream. In this way, from 60 to 75 cubic centimetres may be collected in the course of fifteen minutes. Afterward it becomes somewhat turbid with the debris of disintegrated food, from which it may be separated by filtration. After three hours, it continues to run freely, but much thickened and grumous in consistency, from the admixture of alimentary debris. In six hours it is less abundant, and in eight hours has become very scanty. It ceases to flow altogether in from nine to twelve hours, according to the quantity of food taken. For purposes of examination, the fluid drawn during the first fifteen minutes after feeding should be collected, and at once separated by filtration from accidental impurities.

Physical Properties and Composition of the Gastric Juice.—Gastric juice obtained by this method is a clear, colorless, or faintly amber-colored fluid, of watery consistency and acid reaction. Its specific gravity does not vary much from 1010. It becomes slightly opalescent on boiling.

The following is the composition of the gastric juice of the dog, based on a comparison of analyses by Lehmann, Blondlot, Otto, and Bidder and Schmidt.

Composition of Gastric Juice.

Water	975.00
Free acid	4.78
Pepsine	15.00
Sodium chloride	1.70
Potassium "	1.08
Calcium "	0.20
Ammonium "	0.65
Lime phosphate	1.48
Magnesium "	0.06
Iron "	0.05
	1000.00

Schmidt, in the case which fell under his observation, found the gastric juice of man similar in constitution to the above, except that it contained a larger proportion of water and a smaller proportion of free acid and pepsine, as well as of solid ingredients generally. In the case investigated by Richet, the amount of acid was, on the average, 1.7 per thousand parts; its minimum being 0.5 and its maximum 3.2. Such differences may therefore exist between individuals, or even in the same individual at different times; depending no doubt on the more or less rapid secretion of the watery parts. Observations on the dog show that the proportion of solid ingredients is usually less when the secretion is abundant, and greater when it is in small quantity. In either case the essential constituents are the same.

The most striking physical property of the gastric juice is its acid reaction, by which it is distinguished from all the other digestive secretions and internal fluids of the body. This property depends on the presence of its *free acid.* Notwithstanding that all observers have recognized in the gastric juice a distinct acidity, a singular difference of opinion still exists as to the particular body which gives it this reaction, and especially whether it be a mineral or an organic acid. Repeated analyses have been made by different methods, and each new result has been claimed as decisive on the one side or the other. Many observers (Prout, Dunglison, Enderlin, Schmidt, Ewald, Hoppe-Seyler) regard the free acid of the gastric juice as hydrochloric acid. Their conclusion is mainly based on the fact that the total quantity of hydrochloric acid obtainable from the secretion is more than sufficient to saturate all the alkaline and earthy bases which it contains. Others (Lehmann, Leuret and Lassaigne, F. G. Smith, Laborde, Bernard and Barreswil) consider the acid ingredient to be lactic acid. In support of this view they adduce certain reactions of the gastric juice which do not belong to solutions of hydrochloric acid, such as precipitation of lime oxalate on the addition of a little oxalic acid,* and the fact that

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* Bernard. Leçons de Physiologie Expérimentale. Paris, 1856, p. 396.

gastric juice does not convert cane-sugar into glucose at a boiling temperature as hydrochloric acid would do.* It is acknowledged that both the acids in question may be obtained from gastric juice by distillation and analysis; † but it is considered doubtful whether the hydrochloric may not be liberated by decomposition, or the lactic produced by fermentation, during the process. Finally, Richet ‡ has investigated the subject by a method which avoids prolonged chemical manipulation. This method depends on the comparative solubility in ether of organic and mineral acids. The organic acids are readily soluble in this menstruum, and ten volumes of ether, shaken up with one volume of a watery solution, will remove from it one-half the lactic acid which it contains. The mineral acids, on the other hand, are but slightly soluble in the same fluid; and it requires 500 volumes of ether to extract from a watery solution one-half its acid ingredient, should this be hydrochloric acid. From experiments of this kind the author concludes that the fresh gastric juice, unmixed with food, contains almost exclusively hydrochloric acid; the proportion being not more than one part of lactic acid to twenty parts of hydrochloric; but that if kept for some days the organic acid may so increase as to preponderate over the mineral; and furthermore, that gastric juice, if mixed with food, may form organic acids during digestion to the amount of one-third or one-half the mineral acid present. The subject, therefore, is not altogether free from obscurity.

It is certain, however, that the normal free acid of the gastric juice, if neutralized, may be replaced by either lactic or hydrochloric acid without impairing its digestive properties. Other acid bodies, both mineral and organic, as dilute sulphuric, nitric, or acetic acids are also available for the purpose, though much less so than the foregoing; while phosphoric, oxalic, and tartaric acids, according to Lehmann, are nearly inert in this respect.

The remaining characteristic ingredient of the gastric juice is its albumenoid matter, known under the name of *pepsine.* This is the special ferment produced by the gastric follicles, to which the peculiar digestive properties of the secretion are due. It is precipitable from the gastric juice by alcohol in excess, and after precipitation may be redissolved in water with its qualities unchanged. Gastric juice is essentially an acidulated solution of pepsine. Both the ferment and the acid must be present in order that the secretion may exert its digestive power. If fresh gastric juice be neutralized by the addition of an alkali or alkaline carbonate, it becomes inactive notwithstanding the presence of pepsine; but its activity may be restored by acidulation. On the other hand, gastric juice from which the pepsine has been thrown down, or in which it has been rendered inactive by boiling, has no digestive power although its acidity remains.

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* Revue des Sciences Médicales. Paris, 1878, tome xii., p. 715.

† Hoppe-Seyler. Physiologische Chemie. Berlin, 1878, p. 215.

‡ Comptes Rendus de l'Académie des Sciences. Paris, 1877, tome lxxxiv., p. 1514.

Both the essential constituents of the gastric juice are produced by the mucous membrane, but their mode of production is different. Pepsine is continuously formed by the nutritive process, and accumulates during the intervals of digestion in the glandular cells. The free acid, on the other hand, appears in quantity only at the time of digestion, and is poured out with the watery constituents of the secretion. There is evidence that it is not present in the immediate product of the glandular cells, but is produced by a rapid change in the fluid after secretion. The mucous membrane is never distinctly acid in its deeper and middle parts, but only on its free surface. This was shown by Bernard,* who injected into the jugular vein of a rabbit two solutions, one of iron lactate, the other of potassium ferrocyanide. These salts would remain unaltered in neutral or alkaline fluids, but in presence of a free acid would unite to form Prussian blue (iron ferrocyanide). On killing the animal, three-quarters of an hour afterward, no blue coloration was found anywhere excepting in the stomach; and in this organ it was confined to the free surface of the mucous membrane, not being perceptible in the substance of the glandules. As both salts must have exuded from the blood-vessels of the mucous membrane, it is evident that it was only at or near its upper surface that they met with sufficient free acid to cause their combination. According to Brunton † a horizontal section through the lower part of the gastric glands of the pigeon, if tested by litmus-paper, shows a neutral or extremely weak acid reaction, while the inner surface of the stomach is strongly acid. The materials of the free acid of the gastric juice are therefore furnished by the alkaline blood; but the acid itself originates by some change in the products of exudation.

A necessary condition for the action of the gastric juice is a certain *temperature.* It may go on more or less rapidly within varying limits, but its most favorable temperature is that of the living body. It is suspended at or near the freezing-point, becomes more active with the increase of warmth, and is at its maximum about 38° C.; above which it again diminishes, and is totally arrested at the boiling temperature. The favorable influence of moderate warmth has been shown by Schiff, ‡ who made two acidulated digestive infusions, and placed in each the same quantity of coagulated albumen; one of the infusions being allowed to remain at a temperature varying from 10° to 17° C., the other being introduced, in a closed glass tube, into the stomach of a living dog. The second was found to have digested in six hours as much albumen as the first at the end of three weeks.

A further peculiarity of the gastric juice is its *resistance to putrefaction.* While other animal fluids, as the saliva, bile, pancreatic juice, mucus, and blood, enter into putrefaction with great readiness, gastric juice may remain exposed to the air at ordinary temperatures for

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* Liquides de l'Organisme. Paris, 1859, tome ii., p. 375.

† Handbook for the Physiological Laboratory. Philadelphia, 1873, p. 491.

‡ Leçons sur la Physiologie de la Digestion. Paris, 1867, tome ii., p. 19.

months without developing any putrescent odor or losing its characteristic properties. It becomes somewhat darker in color, and after a time deposits a brownish sediment, but retains its acid reaction and its power of digesting albuminous matters. It will even arrest putrefactive changes which have already begun in organic substances; and consequently putrefaction does not go on in the living stomach. Beaumont preserved fragments of meat unaltered for a month in gastric juice, while other portions kept in saliva were putrefied in ten days. Spallanzani found in the stomach of a viper the body of a lizard which had remained there for sixteen days without putrefactive alteration; and similar observations have been made by other physiologists. According to Richet, the antiseptic property of gastric juice depends entirely on its free acid, and not in any degree on its organic ferment.

Pepsine Extracts, and Artificial Digestive Fluids.—As the immediate source of the gastric juice is the mucous membrane of the stomach, the idea was early suggested that a similar fluid might be extracted from its tissue after death. Experiments of this kind have been made in various ways since 1834; and they have demonstrated that the gastric mucous membrane, taken from the recently-killed animal, may yield a solution containing pepsine, which, in the presence of a dilute acid, at the proper temperature, has the power of dissolving solid albuminous matters. Such solutions act as artificial digestive fluids, and by their use much additional light has been thrown on the digestive process. They are obtained, according to Lehmann's method, by immersing the cleansed mucous membrane in water for an hour or two, until moderately softened, when its glandular parts are removed by scraping with a spatula, placed in acidulated water, the mixture kept for an hour at the temperature of 35° C. and the fluid then filtered. Or the mucous membrane may be cut into small pieces, and kept in a large quantity of acidulated water at 35° C. until the glandular tissue is fully disintegrated, when the mixture is filtered and the clear liquid used for experiment. The second process yields a fluid which has considerable digestive activity, but is contaminated with products of the digestion of the stomach tissues. The most convenient and most widely employed method is that of Von Wittich, which consists in extracting the mucous membrane with glycerine. It has the advantage that glycerine, in the concentrated form, while it dissolves out the pepsine, arrests completely both digestive and putrescent alterations. The extract finally obtained is therefore free from the products of digestion, and may be kept indefinitely for experimental use. In this process the mucous membrane, cut into small pieces and freed from water by a short immersion in alcohol, is placed in a quantity of glycerine sufficient to cover it and macerated for eight days at ordinary temperatures, after which the glycerine solution is strained off. This glycerine extract contains pepsine, and a little of it added to acidulated water forms an efficient digestive fluid. If desired, the pepsine may be precipitated from the glycerine solution by alcohol in excess, removed by filtration in a comparatively pure condition, and then redissolved in water or an acidulated solution. The proportion of acid best adapted for digestion is about 2 parts hydrochloric acid to 1000 parts of water. The most convenient substance for showing the digestive powers of such a fluid is coagulated fibrine, obtained by whipping fresh blood, and cleansed from coloring matter by repeated washing with cold water.

Physiological Action of the Gastric Juice.—If gastric juice from the living animal, or an acidulated solution of pepsine prepared by the above method, be tested at the temperature of 38° C. with different organic matters, it will be found that its action is confined to those of a single class. It has no effect upon starches or fats; but albuminous matters, such as coagulated fibrine, caseine, or white of egg, or tissues mainly composed of albuminous substances, are softened and liquefied, and finally digested. The process by which this change takes place is twofold, accomplished by the successive or simultaneous action of the two essential constituents of the secretion. The first effect is produced under the influence of the free acid, by which the albuminous matter is converted into *syntonine.* This substance is soluble in dilute acids, and therefore assumes the liquid state in an acidulated solution; but it is not soluble in pure water nor in solutions of the neutral salts, and it may accordingly be precipitated by neutralization with an alkali. So far, the modification of albumen in the digestive act is comparatively simple. Its further change is due to the presence of pepsine. By the influence of this substance, acting as a ferment, the modified albuminous matter is transformed into *peptone.* Since peptone is soluble in pure water and in neutral solutions, as well as in dilute acids and alkalies, it retains the liquid form whatever may be the reaction of the fluid in which it is contained. The non-precipitation of the albumenoid matter, on neutralizing the solution, is therefore the indication and measure of its complete transformation in the digestive process.

As one of the distinctive features of peptone is its diffusibility through animal membranes, it represents the condition of albumen when prepared for absorption by the blood-vessels. It is not coagulable by heat, the mineral acids, nor by potassium ferrocyanide, but is thrown down from its solutions by alcohol in excess.

The characters of peptone are the same, or nearly so, whether it be derived from coagulated fibrine, albumen, caseine, or an organized structure, like muscular or connective tissue. According to Henniger, the only perceptible difference is in its rotary power on polarized light. All varieties of peptone in solution deviate the plane of polarization toward the left; the amount of rotation being greatest for albumen peptone, while that for fibrine peptone is the least. As to its nature, it is the prevalent opinion among physiological chemists, that peptone is a product of hydration; the albuminous molecule uniting with the elements of water under the influence of the gastric ferment. This view is partly based on the elementary composition of peptone and its power of uniting with acids and bases, as compared with albumen. It is also sustained by the experiments of Henniger,* who subjected peptone to a process of dehydration by means of anhydrous acetic acid at 80° C., obtaining as the result an albumen-like substance coagulable by heat.

Digestion of the Stomach Tissues by Gastric Juice.—As the gastric juice, or acidulated pepsine solutions, can dissolve the substance of all albuminous tissues, they have the same effect on the walls of the stomach itself. If the gastric mucous membrane be macerated in acidulated water at the temperature of 38° C., the mixture no sooner absorbs pepsine from the gastric follicles than it becomes digestive, and consequently dissolves the tissue of the membrane itself. It, therefore, requires some explanation to understand how the stomach can produce a secretion which is capable of destroying its own substance. This is, no doubt, due to the manner in which the secretion takes place. We have already seen that pepsine is a constant ingredient of the glandular cells formed in the intervals of digestion, while the free acid is produced by a sudden exudation, on the introduction of food. The acid is also poured out only near the orifices of the glandular follicles, being at once discharged into the cavity of the organ and absorbed by the alimentary mass. The gastric juice can exert its digestive power only in the presence of an acid reaction, and the mucous membrane is consequently protected from its influence by the alkalescence of its interstitial fluid, maintained by the circulation of the blood. The nature of the change by which a free acid is produced from the constituents of the alkaline blood is not certainly known, but there is no doubt that this acid first appears after the exudation of the fluids, and it is also plain that its liberation must increase for the moment the alkalinity of the remaining constituents of the mucous membrane.

But after death self-digestion of the stomach is not an unfrequent occurrence. It does not take place in the majority of cases, because, as a rule, digestion has been suspended during the last hours of life, and the stomach contains little or no gastric juice. On the other hand, when death takes place suddenly, soon after the ingestion of food, and when the body is not too rapidly cooled, the accumulated gastric juice acts on the walls of the stomach as well as on the food which it contains. Owing to the stoppage of the circulation, the local alkalescence of the fluid is no longer maintained, and the free acid at last preponderates over the blood remaining in the capillary vessels. The mucous membrane, thus imbibed with an active digestive fluid, in the course of ten or twelve hours may be so softened and disintegrated as to expose the submucous connective tissue; and occasionally all the coats of the organ have been found destroyed, with a perforation into the peritoneal cavity. After death, accordingly, the tissues of the stomach are affected by the gastric juice in the same way as the albuminous ingredients of the food.

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* Revue des Sciences Médicales. Paris, 1878, tome xii., p. 721.

Daily Quantity of the Gastric Juice.—The quantity of gastric juice secreted during a given time, like that of the saliva, varies much according to the condition of the secreting organ. An exact estimate of its daily amount is difficult for several reasons. First, if excited by artificial irritation of the gastric mucous membrane, its quantity is not so abundant as when produced by the natural stimulus of food; secondly, if excited by the introduction of food, a part of it is absorbed by the alimentary material, and consequently cannot be collected for measurement; and thirdly, the quantity collected during a short period does not indicate the rate of production for the rest of the twenty-four hours, because its secretion is influenced by the state of the digestive process. Neither can we draw from a fistula all the gastric juice obtainable during twenty-four hours, and consider that as representing the normal daily amount; because we should be taking away a quantity of fluid which is naturally retained for reabsorption by the blood-vessels, and its supply would be consequently diminished. But notwithstanding these difficulties, sufficient facts have been collected to show that the gastric juice is far more abundant than the other digestive fluids. Beaumont obtained from the stomach of St. Martin, by the introduction of a gum-elastic catheter, 44 grammes of gastric juice in fifteen minutes. We have often collected from a medium-sized dog, at the beginning of digestion, from 60 to 75 grammes in the same time. Bidder and Schmidt, in a dog weighing 15.5 kilogrammes, obtained by separate experiments, consuming in all twelve hours, 793 grammes of gastric juice. If these experiments, as is probable, indicate the average rate of secretion during the day, the entire quantity for twenty-four hours, in an animal of that size, would be 1586 grammes; or about 100 grammes for every kilogramme of bodily weight. By applying this calculation to a man of ordinary size the authors estimate the average daily quantity of gastric juice in man at about 6500 grammes. Schmidt, in his case, already quoted, of a woman with gastric fistula, obtained, as the mean result of several observations, 580 grammes of gastric juice in the course of an hour. The secretion, however, was much poorer in characteristic ingredients than that usually obtained from the dog, and was also inferior in digestive power.

Another method for estimating the daily quantity of gastric juice is to ascertain the amount required for digesting the albuminous food. According to Lehmann,* one gramme of coagulated albumen, calculated as dry, requires for its solution 20 grammes of gastric juice. As the average daily consumption of albuminous matter in man is 130 grammes, this would require 2600 grammes of gastric juice per day. Our own observations on the digestibility of fresh meat make the daily requirement higher. A weighed quantity of fresh lean meat, containing 78 per cent. of water and 22 per cent. of solid ingredients, was cut into small pieces, and digested for ten hours, with frequent

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* Physiological Chemistry. London, 1853, vol. ii., p. 53.

agitation, in a measured quantity of fresh gastric juice at the temperature of 38° C. The liquefied portions were then filtered away, the residue evaporated to dryness, and the quantity of fresh meat remaining undissolved thus calculated from the percentage of its solid ingredients. In this way it was found that one gramme of meat had been liquefied by 13.5 grammes of the digestive fluid. We have already seen (p. 129) that a man consumes, in his ordinary daily ration, 453 grammes of meat; which would require for complete digestion a little over 6000 grammes of gastric juice. This agrees very nearly with the estimate of Bidder and Schmidt given above; and if gastric juice were the only digestive fluid acting on the food, we might accept it as correct. But below the stomach other secretions take part in the digestive process; and some of them, especially the pancreatic juice, have a certain action on albuminous matters, and may facilitate considerably their solution in the intestine. For the partial solution of meat, the disintegration of its fibres, and its reduction to a soft, grumous, or semi-fluid consistency, Beaumont found a much smaller quantity of gastric juice sufficient. In one experiment, one gramme of cooked meat was disintegrated by 2.5 grammes, and in another by 1.83 grammes of gastric juice. Its complete solution would of course require a larger quantity.

These data are insufficient for determining the precise quantity of gastric juice required for digestion. But if we allow sufficient weight to all the observations on this subject, it is evidently very abundant; and it would not be extravagant to estimate its quantity as at least 3000 grammes per day.

Process of Stomach Digestion.—The first effects of the introduction of food into the stomach, according to all observers, are increased vascularity of its mucous membrane, a slight elevation of its temperature, and the exudation, in greater or less abundance, of its acid secretion. At the same time the *peristaltic movement* begins to take place, by the alternate contraction and relaxation of the longitudinal and circular fibres of the muscular coat. This motion is minutely described by Beaumont, who examined it, both by watching the movements of the food through the gastric fistula, and by introducing into the stomach the bulb and stem of a thermometer. According to his observations, the food, after entering the cardiac orifice, is first carried to the left into the fundus of the stomach, thence downward and along the great curvature to the pyloric portion. In this region there was often a constriction, by which the thermometer was gently grasped and drawn, with a twisting motion, toward the pylorus. In a moment or two, it was again released and carried, together with the food, along the small curvature of the organ to its cardiac extremity This circuit was repeated so long as any food remained in the stomach; but toward the end of digestion it became less active, and the stomach, when completely empty, returned to its ordinary quiescent condition.

The muscular action of the stomach during digestion in the dog may be observed by means of a gastric fistula. A metallic catheter, introduced through the fistula when the stomach is empty, must usually be held in place, or it will fall out by its own weight. But on the introduction of food, the catheter is grasped and retained with some force, by the contraction of the muscular coat. A twisting motion of its extremity may also be frequently observed, similar to that described by Beaumont. This peristaltic action, though quite gentle, is sufficient to produce a churning movement of the food, by which its different portions are shifted from side to side, and the gastric juice made to penetrate thoroughly all its parts. It thus receives a more rapid and uniform digestion of its various ingredients. The movement is one which cannot be fully imitated in experiments on artificial digestion in test-tubes; and the process, under these circumstances, is consequently less rapid than in the interior of the stomach.

The alimentary matters, thus incorporated with the gastric juice, are *disintegrated by the liquefaction of their albuminous ingredients.* Bread consists mainly of hydrated starch and solid gluten. By digestion the gluten is converted into soluble peptone, the starch being thus set free, and the whole reduced to a diffluent condition. The same effect is produced on bread subjected to the action of gastric juice in a test-tube, the gluten passing into a liquid condition, while a deposit of unaltered starch settles at the bottom. Cheese, consisting of coagulated caseine and milk globules, undergoes an analogous change. Its caseine is liquefied, while its liberated fat globules rise to the upper part of the fluid, forming a creamy-looking layer on its surface.

Adipose tissue is disintegrated by the liquefaction of its fibrous and membranous parts, while the fatty matter escapes in the form of oil drops, floating upon the other contents of the stomach. Beaumont always found free oil globules, thus extricated from the fatty tissues soon after they had been taken with the food; and it is easy to verify this observation, either by artificial digestion of adipose tissue in gastric juice, or by opening the stomach of an animal after the administration of food containing fat.

The digestion of *muscular flesh* is also at first a process of disintegration. The connective tissue surrounding the fibrous bundles yields to the action of the gastric juice, and the fibres become separated, forming a gruelly mixture of microscopic threads and fragments. The fibres then break up, and, when examined by the microscope, are found to have lost the distinctness of their transverse striations. In food which has been thoroughly masticated, this change goes on rapidly and uniformly throughout the mass. If, as in the dog, the meat be swallowed without much mastication, or if portions be suspended in a test-tube with gastric juice, the digestive action progresses from without inward. The external parts are first softened and decolorized, becoming covered with a grayish layer, of grumous consistency, containing the isolated fragments of muscular fibre. As these portions are removed, the action extends to the parts beneath, and so on until the whole is reduced to a uniform mixture, of gruelly consistency, in which only remnants of the muscular fibres can be detected by the microscope. It is this apparently homogeneous, pultaceous, or semi-fluid material that was formerly designated by the name of "chyme." It is a mixture of disintegrated and semi-digested tissues, portions of which have been liquefied while others are not yet reduced to a state of solution.

Milk, when taken into the stomach in a fresh condition, is first coagulated, afterward dissolved. The preliminary coagulation of its caseine, under the influence of the gastric juice, takes place very rapidly. Beaumont found that milk could be withdrawn in a coagulated condition fifteen minutes after its introduction into the stomach; and that if the mixture were kept at the temperature of 38° C., the coagula were again liquefied in the course of eight hours. The coagulation of milk, by contact with the gastric juice, is in the form of minute, soft flocculi, which, at the temperature of the body, readily undergo the conversion into peptone, and are thus redissolved. Milk, as used by adults, in various culinary preparations, is generally incorporated, in the coagulated form, with other articles of food.

The *vegetable tissues*, as a rule, are digested in a manner similar to that described above. The albuminous matters are dissolved out, leaving the starchy and oleaginous ingredients in a free condition, but chemically unchanged. As these tissues generally contain a smaller proportion of albuminous matter than animal food, the main result of the changes which they undergo in the stomach is their disintegration.

The gastric juice, after commencing its action in the stomach, *passes*, with the debris of the food, *into the intestine*. This can be seen in the dog by killing the animal after feeding, and examining the contents of the alimentary canal. The same thing may be observed by means of a duodenal fistula, established by an operation similar to that for fistula of the stomach. A silver tube, with flanges at each end, is introduced into the lower part of the duodenum, and the wound allowed to heal, after which the contents of the intestine may be withdrawn and examined at different periods of digestion.

About half an hour after the ingestion of a meal, the gastric juice begins to pass into the duodenum, recognizable by its strongly-marked acidity, and containing a certain quantity of peptone in solution. It soon afterward becomes mingled with the debris of muscular fibres, fat vesicles, and oil drops; substances easily recognizable under the microscope, and which produce a grayish turbidity in the fluid withdrawn from the fistula. By the continuous passage, in this way, of alimentary material, mixed with gastric juice, the stomach becomes gradually cleared of its contents. In the experiments of Beaumont the time required for the disappearance of food from the stomach varied from one hour to five hours and a half, according to the quality and quantity of the material used. In those of Prof. F. G. Smith on the same subject, food seldom remained in the stomach more than two hours after its introduction. Three hours is probably sufficient, as a rule, for complete stomach digestion, in man, when the food is in moderate quantity and has been properly prepared by cooking and mastication. In the dog, where the food is generally swallowed in fragments of some size, the process is longer; and a moderate meal of fresh uncooked meat requires from nine to twelve hours for its liquefaction and disappearance from the stomach.

The gastric juice, after accomplishing its work in digestion, is *reabsorbed* from the alimentary canal by the blood-vessels. It forms a vehicle for the dissolved nutritious material, and again enters the circulation, bringing with it the alimentary substances in solution. An abundant supply of the secretion may therefore be poured out during digestion, at an expense to the blood, at any one time, of only a small quantity of fluid. The simplest investigation shows that neither gastric juice nor peptones accumulate to any considerable amount in the stomach; each portion of the food, when digested, being disposed of by absorption, together with its solvent fluid. There must be accordingly, during digestion, a continuous circulation of fluids from the blood-vessels to the alimentary canal, and from the alimentary canal back again to the blood-vessels.

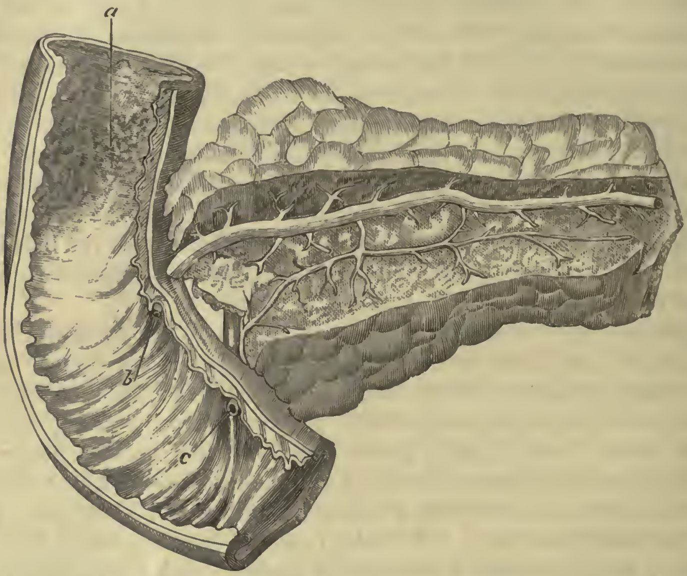
That this really takes place is shown by the following facts: First, if a dog be killed some hours after feeding, there is never more than a very small quantity of fluid found in the stomach, just sufficient to smear over and penetrate the half digested pieces of meat; and secondly, in the living animal, gastric juice, drawn from the fistula five or six hours after digestion has been going on, contains little or no more peptone in solution than that extracted fifteen or twenty minutes after the introduction of food. To obtain gastric juice saturated with alimentary matter, it must be artificially digested with food in test-tubes, where absorption and renovation cannot take place.

The secretion of gastric juice is much influenced by *nervous conditions.* It was noticed by Beaumont, in his experiments with St. Martin, that irritation of the temper or other moral causes would often diminish or suspend the supply of the gastric fluids. Any febrile action or unusual fatigue would exert a similar effect. Every one is aware how readily mental disturbances, such as anxiety, anger, or vexation, will take away the appetite and interfere with digestion. Impressions of this kind, especially at the commencement of the process, seem liable to produce a lasting effect and to disturb digestion for the entire day. In order, therefore, that the function may be properly performed, food should be taken only when the appetite demands it; it should be thoroughly masticated; and, finally, both mind and body, particularly in the early part of digestion, should be free from unusual or disagreeable excitement.

Pancreatic Juice.

The pancreas, which is similar in general structure to the salivary glands, lies across the upper part of the abdomen, with its larger or right-hand extremity in contact with the duodenum. It is traversed longitudinally by a main excretory duct, receiving, as it passes from left to right, lateral branches from the glandular lobules, and opening into the duodenum next to the orifice of the common biliary duct, about ten centimetres below the pylorus. Its secretion thus mingles with the products of stomach digestion, almost immediately after they have passed into the duodenum.

Fig. 25.



Portion of Human Pancreas and Duodenum.—*a*. Cavity of duodenum. *b*. Orifice of the pancreatic duct. *c*. Orifice of lower pancreatic duct. (Bernard.)

The arrangement of the gland and its duct, in the lower animals, is in most respects similar to the above. In the dog and cat, there are two ducts opening into the intestine, one in juxtaposition with the biliary duct, the other from one to three centimetres farther down. The lower duct is usually in these animals, though not always, the larger of the two, and they generally communicate with each other in the substance of the gland by a transverse branch. Even in man, as shown by Bernard, Kölliker, and Sappey (Fig. 25), there is often a small accessory duct opening into the intestine, sometimes above and sometimes below the principal excretory orifice. The most marked peculiarity of these parts is in the rabbit, where the single pancreatic duct opens into the intestine 30 or 40 centimetres below the biliary duct.

The pancreatic juice is obtained from the living animal by opening the abdomen, and inserting a canula into the main pancreatic duct, immediately before its entrance into the intestine. The canula being secured in position by a ligature placed around the duct, the parts are returned to the abdominal cavity, the external wound closed with sutures, and the extremity of the canula left projecting between its edges. The secretion is thus diverted from the intestine, and may be collected as it flows from the canula. The operation has been most frequently performed on the dog, but it has also been done on the rabbit, the ox, the sheep, the goat, the pig, and the goose. The secretion has been obtained from the horse, by opening the duodenum and inserting a canula in the orifice of the pancreatic duct.

The fistula produced by this means is a temporary one, as the ligature soon cuts its way through the duct, and the canula is displaced; the communication of the duct with the intestine soon becoming re-established. In the ox, this happens within six or eight days after the operation; and in the dog, according to Bernard, within three days. As the pancreas, furthermore, is very sensitive to irritation and its secretion liable to alteration by the inflammatory process, it should be collected for examination within twenty-four hours after the insertion of the canula.

Physical Properties and Composition of the Pancreatic Juice.— Pancreatic juice, obtained from the dog in the above manner, during digestion, is a clear, colorless fluid, distinctly alkaline, with a well marked viscid consistency, like fluid white of egg. Owing to the abundance of its albumenoid ingredients, it coagulates completely at the boiling temperature, often solidifying into a jelly-like mass. It also assumes a gelatinous consistency on being cooled down to 0° C., again liquefying when raised to the ordinary temperature. According to Schmidt,* it has the following composition:

COMPOSITION OF PANCREATIC JUICE.

Water	900.76
Albumenoid substances	90.44
Sodium chloride	7.35
Potassium chloride	0.02
Lime phosphate	0.41
Magnesian phosphate	0.12
Soda, lime, and magnesia, in organic combination	0.90
	1000.00

The pancreatic juice resembles a solution of albumen in being coagulable by heat, by mineral acids, and by alcohol in excess. It presents, however, the important distinction that its organic matter, after being precipitated by alcohol, is again soluble in water. This substance is, therefore, different in character from ordinary albumen, notwithstanding the similarity in some of its reactions.

A striking peculiarity of this secretion, due to the presence of its albumenoid matter, is its property of emulsioning neutral fats. If a few drops of oil be shaken in a test-tube with fresh pancreatic juice, it is instantaneously broken up into a permanent uniform emulsion; and if the oil be in slight excess it forms, after a time, an opaque creamy layer upon the surface, the greater part remaining diffused through the

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* Annalen der Chemie und Pharmacie. Heidelberg, 1854, Band xcii., p. 33.

mixture. The pancreatic juice acts in this way like a solution of albumen. Its emulsifying power is not due to its alkaline reaction, but to the organic matter which it contains; since its alkalescence may be neutralized, as shown by Bernard,* without sensibly impairing its activity in this respect. The instantaneous effect thus produced on the fats is limited to their emulsion. They are disseminated through the fluid in the form of minute particles, but their chemical characters are not altered until other changes occur at a later time.

Among the albumenoid ingredients of the pancreatic juice are substances belonging to the class of ferments, which exert three distinct actions on alimentary substances; namely, a transforming action on starch, a digestive action on coagulated albumen, and a partial acidifying action on fats. All these substances may be precipitated by alcohol from pancreatic juice, or extracted by water or by glycerine from the pancreatic tissue; but they have not been obtained in a state of purity, or even distinctly separated from each other, to the satisfaction of physiological chemists.

The first of these substances, the so-called *pancreatine*, is a diastatic ferment; that is, it has the power, like vegetable diastase, of transforming starch into glucose. It produces this change very readily at the temperature of the body, and it may be preserved under alcohol or in glycerine for an indefinite time without losing its properties. When dry, it may be heated to 100° C., and still retain its catalytic power; but in watery solution, it is coagulated and rendered inactive by a boiling temperature. It is produced in the gland, probably by the transformation of some previously formed substance, since it has been found by Liversidge,† that after it has been completely extracted by glycerine from the chopped glandular tissue, the inactive residue, if exposed to the air for five or six hours, will regenerate the ferment, so that it may again be extracted by water or glycerine. This ferment exists in the pancreas and the pancreatic juice of every animal thus far examined. The second ferment, known as *trypsine*, is that which causes the solution of albumenoid matters. This property of the pancreatic juice, first observed by Bernard and Corvisart, has been the subject of many experiments, among the most valuable of which are those of Kühne.‡ This observer operated both with the pancreatic juice of the dog and with infusions of the glandular tissue. He found that the fresh viscid secretion could, in from half an hour to three hours, effect the solution of coagulated fibrine and albumen, without modification of its alkaline reaction. If the process be arrested at this point no putrefactive changes take place in it; but if continued for a longer time, it gives rise to the products of decomposition. The activity of this ferment is greatest in an alkaline solution; it goes on, though with less energy,

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* Liquides de l'Organisme. Paris, 1859, tome ii., p. 346.

† Studies from the Physiological Laboratory of the University of Cambridge, Part I. Cambridge, 1873, p. 49.

‡ Archiv für pathologische Anatomie und Physiologie, 1867, xxxix., p. 130.

in a neutral mixture; and is nearly or quite suspended in the presence of a dilute acid. Under favorable conditions it dissolves not only coagulated fibrine and albumen, but also the substance of animal tissues. In his experiments with the tissue of the pancreas, Kühne placed the finely divided gland in warm water, with a weighed quantity of the substance to be experimented on; allowing the infusion of the pancreas and the digestion of the albuminous matter to proceed simultaneously. He found that when employing for this purpose a dog's pancreas of from 50 to 60 grammes weight, 400 grammes of boiled and pressed fibrine were reduced to an insignificant residue in from three to six hours, the reaction of the mass continuing faintly alkaline.

The action of the pancreatic ferment on albumenoid matters differs from that of pepsine in its details, but is the same in its result. If coagulated fibrine be immersed in pancreatic juice or an alkaline trypsine solution, it does not become swollen and gelatinized, nor is it transformed into syntonine as it would be in gastric juice. The pieces of fibrine become rather shrivelled and condensed, and are afterward liquefied without passing through the modification of syntonine. But when liquefaction is accomplished, the substance in solution has all the characters of peptone, in the same degree as if produced by stomach digestion—its non-coagulability by heat, its solubility in water, in dilute acids and alkalies, and in neutral solutions, and its diffusibility through animal membranes. The final change produced by trypsine in albumenoid substances appears, therefore, to be a hydration, but effected by a different process from that of digestion with gastric juice.

It seems evident, accordingly, that the pancreas during life produces a ferment which is capable of dissolving its own tissue. The difficulty of accounting for such a fact is greater in this case than in that of the stomach; since the pancreatic ferment is most active in presence of an alkaline reaction, like that of the blood and the interstitial fluids of the tissues. It is indicated by the experiments of Haidenhain that trypsine is not contained under its own form in the glandular cells during life, but is produced, at the moment of secretion or after death, from a preexisting inactive substance, termed "zymogen." There are, no doubt, such preliminary stages in the formation of all ferment bodies; but the trypsine ferment is actively present in freshly secreted pancreatic juice, and its mode of production from the preceding inert material must be for the most part a matter of surmise. The pancreas does not appear liable, like the stomach, to self-digestion after death, though the surrounding conditions would seem often favorable to such an alteration.

The third substance of this kind in the pancreatic juice, causing decomposition of the neutral fats, with liberation of a fatty acid, has not received a distinct name. It is known, however, by its action whenever fresh pancreatic juice, an infusion of the pancreas, or its moist tissue, is brought in contact with liquid neutral fat at the temperature of 35° to 40° C. In a short time an acid reaction becomes manifest, sufficient to redden blue litmus-paper, and on keeping the mixture at the above temperature, the quantity of acid increases. Bernard and Bertelot* have shown that in this process the fat is decomposed into a fatty acid and glycerine. A few decigrammes of neutral fat, emulsified with 20 grammes of fresh pancreatic juice from the dog, and kept at a moderately warm temperature, were almost completely acidified at the end of twenty-four hours, leaving only about one-tenth part of undecomposed fat. The change which occurs when fat is replaced by a fatty acid and glycerine, is as follows:

$$\overset{\text{Stearine.}}{C_{57}H_{110}O_6} + \overset{\text{Water.}}{3\,(H_2O)} = \overset{\text{Stearic Acid.}}{C_{54}H_{108}O_6} + \overset{\text{Glycerine.}}{C_3H_8O_3}$$

It includes, therefore, a hydration, and cannot take place except in the presence of water. If the experiment be performed with pancreatic juice of normal alkaline reaction, or with alkaline infusions of the pancreas, a portion of the acid set free is saponified by union with the alkaline bases. The chemical change accordingly is the same as that in the saponification of fats by continued boiling with water and an alkali; the ferment of the pancreatic juice, in a short time and at a moderate warmth, taking the place of prolonged ebullition in its influence on the fats.

According to Wurtz and Hoppe-Seyler, this ferment, unlike the two preceding, is insoluble in glycerine, and is rendered inactive by contact with alcohol. Its action can be studied only in the pancreatic juice, or in watery infusions of the glandular tissue; and its physical qualities and composition are even more imperfectly understood than those of other bodies of the same class.

Mode of Secretion and Daily Quantity of the Pancreatic Juice.—When examined in the living animal by means of a canula introduced into its excretory duct, it is found that the action of the pancreas varies much in activity at different times. In the intervals of digestion, or if the process be temporarily arrested from any cause, no fluid whatever is discharged from the canula. When digestion is in progress, the pancreatic juice soon begins to run from the orifice of the tube, at first slowly and in drops. Sometimes the drops follow each other with rapidity for a few moments, after which the discharge is suspended. It then recommences, and continues to exhibit similar fluctuations during the whole course of the experiment. Its flow, however, is at all times scanty, as compared with that of the gastric juice. We have never been able to collect, in a dog of medium size, more than 75 grammes in three hours, and usually the quantity has been much less than this. Colin found a great variation in the animals on which he experimented, the quantity being from two and a half to thirty times as abundant at one period as at another. In the bullock, while ruminating, the largest quantity obtained was 342 grammes per hour.

The entire quantity of pancreatic juice per day cannot therefore be determined with precision, but it is evidently moderate in amount, as

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* Bernard, Leçons de Physiologie Expérimentale. Paris, 1856, p. 263.

compared with the other digestive fluids. In the ox, cow, and horse, Colin found the average quantity nearly the same, corresponding to about 0.58 gramme per hour for every kilogramme of bodily weight. Schmidt found it, in the dog, not more than 0.2 gramme per kilogramme per hour. In the most successful instances, we have found it, in the dog, as much as 1.25 gramme per kilogramme per hour during digestion, but much less than this in the intervals. If we take, as the average of these estimates, 0.5 gramme per hour for every kilogramme of bodily weight, it would give for a man of medium size about 800 grammes as the entire quantity secreted per day.

The condition of the pancreas varies at different periods corresponding with the activity of its secretion. In the intervals of digestion it is pallid and dense; during digestion it becomes turgid and vascular, its ruddy color showing the increased quantity of blood in its vessels. According to most observers, the ferment which effects the solution of albuminous matters can only be extracted from the pancreas of animals killed during the height of digestive action, which, in the dog, is from five to seven hours after the ingestion of food. When digestion comes to an end, the vascularity of the pancreas diminishes, and the organ returns to its quiescent condition. This periodical excitement at the time of functional activity is observable, not only in the pancreas, but in all parts of the digestive apparatus.

Physiological Action of the Pancreatic Juice—Among the most important effects produced by pancreatic juice in digestion is the *emulsification of the fats.* This action is prompt and efficient when oil is mixed with pancreatic juice in a test-tube, quite unlike anything obtained by similar experiments with saliva, gastric juice, or bile. Bernard found that the fresh pancreatic juice of the dog, at 38° C., would form a complete and permanent emulsion with olive oil, butter, suet, or lard, when mixed with either of these substances in the proportion of one gramme of oleaginous matter to two grammes of pancreatic juice. In the horse, ass, ox, sheep, and pig, according to Colin,* this property of the pancreatic juice is in proportion to the amount of its albumenoid matter; one part of oil requiring for complete emulsion from two to three parts of pancreatic juice when its organic ingredients are abundant, and four, five, or six parts when they are in smaller quantity.

Within the alimentary canal the emulsive action of the pancreatic juice is equally well marked. The fats are not affected by either saliva or gastric juice; and examination shows that they are unchanged in their essential characters so long as they remain in the stomach. In this organ they are simply liquefied by the warmth of the body, and set free by the solution of their albuminous envelopes; and they are still visible in larger or smaller drops on the surface of the alimentary mass. But almost immediately after passing into the intestine, the

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* Physiologie Comparée des Animaux domestiques. Paris, 1854, tome i., p. 644.

oily portion of the food is altered in appearance, being converted into a white, opaque emulsion, termed *chyle*, always found during digestion entangled among the valvulæ conniventes, and adhering to the surface of the small intestine. The digestion of fatty substances consists mainly in this emulsion, by which they are converted into chyle and made ready for absorption. As the change begins to take place in the duodenum, immediately below the orifice of the pancreatic duct, this circumstance points to the pancreatic juice as the main agent in the formation of chyle. But in most animals the biliary duct opens into the intestine at nearly the same point, and it might therefore be questioned whether the bile has not an equal share in the result. This doubt was removed by the experiments of Bernard on the rabbit. In this animal, the biliary duct opens, in the usual manner, just below the pylorus, while the pancreatic duct communicates with the intestine 30 or 40 centimetres farther down; so that there is a considerable extent of the small intestine containing bile, into which the pancreatic juice has not yet been discharged. Bernard fed these animals with substances containing oil, or injected melted butter into the stomach; and, on killing them afterward, found no chyle in the intestine between the openings of the biliary and pancreatic ducts, while it was abundant immediately below the orifice of the latter. Above this point the lacteal vessels were empty or transparent, while below it they were full of opaque chyle. These experiments, which were confirmed by Jackson,* show that the emulsifying action of the pancreatic juice on oily matters is exerted within the body during digestion, and that it is the direct agent in the production of chyle in the intestine.

It is probable that the *acidifying* action of pancreatic juice on fats is less extensive during digestion than its emulsive effect. These two properties of the secretion, when examined in the test-tube, show a difference in their mode of action. The emulsification of fat, when in contact with pancreatic juice, is instantaneous and complete; but its acidification requires a longer time, and increases progressively for some hours. A partial acidification and saponification undoubtedly takes place in the duodenum; but the greater part of the fat remains in the form of an emulsion, and the absorption of chyle begins immediately below the orifice of the pancreatic duct, as shown by the condition of the lacteal vessels. The chyle in the lacteal vessels is mainly composed of undecomposed fat; and, according to Hoppe-Seyler, the quantity of saponified fat, in both the intestine and the lacteals, is comparatively insignificant.

The second important action of the pancreatic juice in digestion is the *transformation of starch into glucose.* It is much more effective in this respect than the saliva, being almost instantaneous, and converting the whole of the starch at once, while that of the saliva is

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* American Journal of the Medical Sciences. Philadelphia, October, 1854.

gradual and leaves for some time a part of the starch unchanged. Kroeger found that one gramme of fresh pancreatic juice, at the temperature of 35° C., transformed into glucose, within thirty minutes, 4.67 grammes of starch; while, according to our own observations, one gramme of fresh human saliva, mixed at 38° C. with a watery solution containing less than 0.1 gramme of boiled starch, though it gives a manifest sugar reaction in one minute, still contains a large portion of unaltered starch at the end of an hour. According to various observers (Bouchardat and Sandras, Ranke, Gorup-Besanez), pancreatic juice also causes the transformation of raw starch, a property which was found by Bouchardat to be very energetic in the secretion of the common fowl.

Starch which has passed the stomach unchanged is thus promptly transformed into glucose after entering the duodenum. In dogs, fed with a mixture of meat and boiled starch, and killed at various periods after feeding, starch is for a time abundantly recognizable in the stomach without traces of glucose, while in the fluids of the small intestine it is absent and glucose takes its place. According to Langendorff,* exclusion of the pancreatic juice from the intestine in pigeons arrests so completely the digestion and assimilation of starch, that these animals die after considerable emaciation, in from six to twelve days. This secretion is plainly the principal agent in the digestion of starch, and as starchy substances constitute, in man, rather more than one-half the entire food, its function is hardly second in importance to any other in the alimentary canal.

It is less easy to judge of the pancreatic juice, as an agent in the *solution of albuminous matters.* Some writers attribute much importance to this action, owing to its striking character in artificial digestions. But it is hardly safe to assume that these experiments represent fully the phenomena of intestinal digestion. In the alimentary canal a number of different secretions are in operation together or successively, and the properties of each may be more or less modified by the time of its secretion, or the proportion in which it is mingled with the others. The action of pancreatic juice on albumenoids is most marked in an alkaline menstruum, and is diminished or arrested by an acidity less than that of the gastric juice. But the reaction of the small intestine in carnivorous animals, during digestion, is acid. According to Bernard† this is always the case. In our own experiments, with a duodenal fistula in the dog, the fluids of the intestine became acid as soon as the contents of the stomach began to pass the pylorus. According to Schmidt-Mulheim,‡ who operated by killing the animals at various periods after feeding and examining the intestinal contents, the reaction of the dog's small intestine during the digestion of meat

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* Archiv für Anatomie und Physiologie. Leipzig, 1879, p. 26.

† Liquides de l'Organisme. Paris, 1859, tome ii., p. 347.

‡ Archiv für Anatomie und Physiologie. Leipzig, 1879, p. 39.

is always acid, usually even to its lowest portions. Moreover, some of the products of artificial digestion do not occur with the same readiness in the intestine of the living animal. In Kühne's experiments on the artificial digestion of coagulated fibrine by trypsine solutions, about one-half the peptone produced was further decomposed into other products, especially leucine and tyrosine. In the observations of Schmidt-Mulheim, on the contrary, the acid contents of the small intestine in dogs, during the digestion of meat, were very poor in leucine and tyrosine, but abundant in peptone. He concludes that the digestion of albumen is almost wholly performed by the pepsine ferment in an acid menstruum, that is, by the gastric juice; and that the office of the pancreatic juice in this respect is secondary.

Bile.

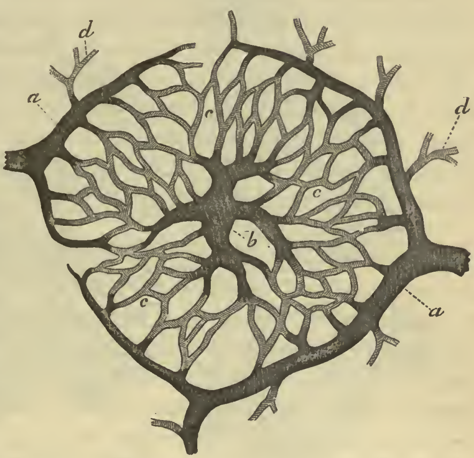
As compared with other accessory glands of the alimentary canal, the liver presents several striking peculiarities. First, its supply of blood is from two different sources; namely, the hepatic artery and the portal vein. The ramifications of the hepatic artery are distributed to the walls of the hepatic ducts and of the portal vein, to the capsule of Glisson and to the peritoneal covering of the organ; while those of the portal vein pass into the glandular parenchyma, and, after traversing its substance as a capillary plexus, become continuous with the rootlets of the hepatic vein. Beside arterial blood, accordingly, which the liver receives in moderate quantity, it is supplied with venous blood in great abundance, conveyed by the portal system from the stomach, the spleen, the pancreas, and the intestine.

Secondly, the liver is distinguished by its size. While the weight of all the salivary glands together, in man, is but little over 100 grammes, and that of the pancreas about 75 grammes, the liver forms a compact vascular and glandular organ, weighing nearly or quite 1600 grammes, and occupying a considerable portion of the abdominal cavity.

Lastly, the liver differs so much in texture from other secretory organs, as to require a special description. The secreting apparatus consists, as usual, of glandular cells and capillary blood-vessels, with ducts for the discharge of the secreted fluid; but these elements, instead of being arranged as elsewhere in distinct groups of tubules or rounded follicles, are closely united, forming on all sides a continuous mass by mutual contact and adhesion.

The substance of the liver is divided into masses or islets, about 1.5 millimetre in diameter, known as the hepatic *lobules*. These lobules, however, are not anatomically separate from each other, but are distinguishable only by the arrangement of the afferent and efferent blood-vessels. Each lobule is embraced by the terminal branches of the portal vein, ramifying between the adjacent lobules, and known as the *interlobular veins*. From the interlobular vein minute vessels pass into the substance of the lobule, forming by their division and inosculation a capillary plexus, the vessels of which have a general convergent direction toward the centre of the lobule. At this point they unite to form an efferent vessel, which, from its position, is termed the *intralobular* vein, and which continues its course until it joins a small branch of the hepatic vein. Each lobule is therefore a more or less ovoid, cylindrical, or prism-shaped mass, resting upon a branch of the hepatic vein. It is attached to this vessel by its own intralobular vein, which passes through its axis receiving the blood collected from it; while it is encircled by terminal branches of the portal vein, which supply the blood for its interior circulation.

FIG. 26.



HEPATIC LOBULE, in transverse section, showing the distribution of its blood-vessels.—*a*, *a*. Interlobular veins. *b*. Intralobular vein. *c*, *c*, *c*. Plexus of capillary blood-vessels within the lobule. *d*, *d*. Twigs of interlobular vein, passing to adjacent lobules.

Beside its capillary blood-vessels, the lobule consists mainly of glandular cells. These are generally of a five- or six-sided prismatic form, often with one or two of their borders excavated by curvilinear furrows at the points where they are in contact with a capillary blood-vessel. They are, on the average, 22 mmm. in diameter, finely granular, usually, in man, containing one or more fat globules, and provided with a round or oval nucleolated nucleus. The cells are everywhere in contact with each other by their plane surfaces, and each one is also in direct relation at several points with a capillary blood-vessel. Thus the two elements are intimately united throughout the substance of the lobule.

There is an equally close connection between the glandular cells and the biliary ducts. The main hepatic duct, which with its ramifications accompanies the divisions of the portal vein, breaks up into branches which finally reach the interlobular spaces. In man, the biliary ducts of a larger diameter than about 200 mmm. are lined with cylindrical epithelium; while in those below 100 mmm. in diameter, the form of the cells changes to that of pavement epithelium. The biliary ducts in the interlobular spaces are of the smaller variety, being not more than 50 mmm. in diameter, and lined with pavement epithelium. They break up into communicating branches, which cover the lobule with a plexus of biliary canaliculi.

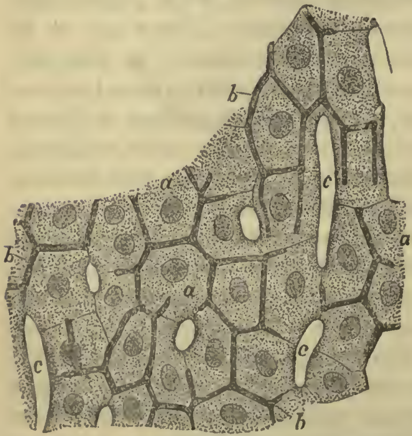
From this superficial plexus the finest biliary tubes penetrate the lobule and there inosculate with each other between the glandular cells.

Fig. 27.

Finer Biliary Canals and Biliary Ducts, from the frog's liver.—*a.* Small biliary duct, with its lining of epithelium cells. *b, c.* Terminal branches of the minute biliary canals, surrounded by glandular cells. *d.* Transverse communicating branch between two biliary canals. *e, e.* Sheath of glandular secreting cells, surrounding the biliary canals *f.* Section of capillary blood-vessel. (Eberth.)

In the amphibia (frogs and water-lizards), as shown by Hering and Eberth (Fig. 27), the ultimate structure of the liver is not essentially different from that of other lobulated glands. The smaller biliary ducts, lined with pavement epithelium, give off minute branches which communicate with each other and are in contact everywhere with the large glandular cells; each terminal branch being surrounded by a single sheath of such cells, representing the epithelial lining of a tube or follicle.

Fig. 28.



Transverse Section of Part of a Lobule from the Rabbit's Liver.—*a, a, a.* Nucleated glandular cells. *b, b, b.* Capillary bile-ducts passing between the adjacent cells. *c, c, c.* Sections of capillary blood-vessels. (Genth.)

In man and the warm-blooded quadrupeds, the texture of the liver is more compact, the glandular cells and capillary blood-vessels more closely united, and especially the finest biliary passages within the lobule are more abundant. From the plexus of canaliculi on the surface of the lobule, smaller branches penetrate its interior, and there inosculate so frequently, that they encircle each glandular cell with their network. These interior communicating passages are the *capillary bile-ducts.* They are much smaller than the capillary blood-vessels, being in the rabbit's liver, according to Kölliker, not more than 2 mmm. in diameter. They embrace the glandular cells in such a way that they are always situated at the greatest possible distance, that is, half the diameter of a cell, from the nearest capillary blood-vessel; the blood-vessels running along the edges of the prismatic cells (Kölliker), while the ducts pass along the middle of their plane surfaces. Thus the two sets of canals, namely, capillary blood-vessels and bile-ducts, form a double series of inosculating passages embracing the glandular cells, and directed at right angles to each other.

Physical Properties and Composition of the Bile.

The bile, as it comes from the gall-bladder, is a clear, more or less ropy fluid, of neutral or alkaline reaction, with a faint animal odor. Its average specific gravity, according to various observers, is about 1020. If shaken with air, it foams up into a frothy mixture, which remains for a long time on its surface. This property depends on the presence of the biliary salts, which have the same action in a watery solution. The ropy character of the secretion varies much at different times, even in the same animals, and is due to the mucus of the gall-bladder; as the bile which flows directly from the hepatic ducts is always a watery fluid. The longer it is retained in the gall-bladder, the more dense and mucous is its consistency.

The color of the bile varies, in different species of animals, from a reddish-orange to a nearly pure green, presenting all the intermediate tints of golden-yellow, reddish-brown, olive-brown, olive, yellowish-green, and bronze-green. Human bile from a biliary fistula was found by Jacobsen to be clear, yellowish, bronze-green; that taken from the gall-bladder after death is usually a dark golden-brown. Dog's bile is brownish-olive or bronze; pig's bile reddish-orange or reddish-brown; and sheep- and ox-bile greenish-olive, or more frequently nearly green. As a rule, the bile of herbivorous animals is more decidedly green, that of the carnivora and omnivora orange or brown. These differences may be referred to two principal tints, corresponding with the two coloring matters of bile; in one of which the predominating color is red or reddish-brown, dependent on *bilirubine*, in the other green, owing to the presence of *biliverdine.* As their proportion varies, the specimen will exhibit a corresponding color of the pure or mingled tints.

The color of the bile is also modified by oxidizing agents, which produce a green hue in olive or brown bile, and increase the intensity of the green when this color is already present. If brown- or olive-colored bile be exposed for a short time, its surface becomes green by contact with the atmosphere. The change may be instantly produced by adding a few drops of a watery solution of iodine; and a little nitric acid acts with great energy, developing at once a bright grass-green hue. The color of green bile, on the other hand, disappears by exclusion of the atmosphere. If ox-bile of a pure green or olive-green hue be inclosed in a full and securely stoppered vessel, so as to be protected from the air, it gradually loses its green color, becoming a dull yellow. The alteration progresses from the external parts of the liquid toward its centre, until at the end of twelve, twenty-four, or thirty-six hours, the whole has become light yellow or yellowish-brown. The green hue may then be restored by the addition of iodine, or by exposing the bile in thin layers to the air. This change depends on the conversion of bilirubine by oxidation into biliverdine.

The bile exhibits a peculiar reaction with nitroso-nitric acid, due to the effect on its coloring matter. If bile be brought in contact, in a cylindrical glass vessel, with a layer of this acid, and allowed to remain without agitation, a series of colored rings are produced at the surface of contact, following each other in definite order, from the bile to the nitric acid, as green, blue, violet, red, and yellow. The colors represent successive stages of the oxidation and final destruction of the coloring matter. This test, known as "Gmelin's bile test," may be applied to other animal fluids in which bilirubine is supposed to be present.

The bile presents, also, certain optical properties which distinguish it from other animal fluids.

First, it is *dichroic;* that is, it has two different colors by transmitted light, according to its mass. If a specimen of ox-bile, which appears of a pure transparent green color by ordinary daylight in layers of two or three centimetres, be viewed by strong sunlight in a thickness of five or six centimetres, it is red. In this respect it resembles a solution of chlorophylle, which presents the same contrast of colors in a very marked manner.

Secondly, it is *fluorescent;** that is, it becomes faintly luminous with a color of its own, when viewed by the more refrangible rays of the solar spectrum. If a specimen of clear greenish bile be placed in the track of either the violet or the blue ray of the solar spectrum, it becomes visible with a light yellowish-green tint. In the green it is more yellowish; and in the yellow it has a tinge of red. Thus in all parts of the spectrum where it exhibits this property, it emits a light of less refrangibility than that of the ray by which it is illuminated. Fluorescence is also manifested, to a remarkable degree, by solutions of chlorophylle, which, although of a clear green color by diffused daylight, are pure red, when viewed by either the violet, blue, green, or yellow ray of the spectrum.

The fluorescence of bile does not depend on its coloring matter, but is due mainly to the biliary salts, since it is also exhibited by their

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* This property, so called from *fluor spar*, in which it was first observed, is shown by various transparent substances, when illuminated by solar light, or by that of certain parts of the spectrum. Thus a solution of quinine sulphate, which is colorless in ordinary daylight, becomes blue where the sun's rays are concentrated upon it by a lens; and it exhibits a distinct luminosity in both the violet and ultra-violet parts of the spectrum.

watery or alcoholic solutions; the only difference being that the color of the solutions by the violet and blue rays is nearly pure yellow instead of yellowish-green.

The bile of the inferior animals can be taken in a state of freshness and purity, and in sufficient quantity for examination, from the gall-bladder immediately after death. It has also been collected by means of an artificial fistula of the gall-bladder or of the common biliary duct. Human bile, taken from the gall-bladder some hours after death, is liable to be more or less altered from its normal condition. It has been obtained in cases of accidental biliary fistula in man by Ranke[*] and Jacobsen.[†] According to Jacobsen its solid ingredients amount to about 22.5 parts per thousand; a little over one-third consisting of mineral salts, the remaining two-thirds of organic matter. Both the coloring matters were always present. The proportions of all the ingredients were as follows:—

Composition of Human Bile, according to the Analyses of Jacobsen.

	Water	977.40
Organic matters.	Sodium glycocholate	9.94
	Cholesterine	0.54
	Free fats	0.10
	Sodium palmitate and stearate	1.36
	Lecithine	0.04
	Other organic matters	2.26
Mineral salts.	Sodium chloride	5.45
	Potassium chloride	0.28
	Sodium phosphate	1.33
	Lime phosphate	0.37
	Sodium carbonate	0.93
		1000.00

In ox-bile, as shown by Berzelius, Frerichs, and Lehmann, the proportion of both mineral and organic ingredients may be much greater than the above, the biliary salts alone amounting to 90 parts per thousand. Ranke found the average proportion of solid ingredients 31.6; and according to Robin[‡] and Hoppe-Seyler,[§] the biliary salts in human bile from the gall-bladder may amount to from 30 to 100 per thousand parts. In Jacobsen's case the specific gravity of the bile was but little over 1010; and we have found it, in human bile from the gall-bladder, 1018. The general result of observations on this point is that the bile becomes more concentrated in the gall-bladder, but acquires no further ingredient except mucus.

The most important constituents of the bile, so far as known, are the biliary salts, sodium glycocholate and sodium taurocholate, already described in Chapter VI. These salts are associated in the bile in

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[*] Physiologie des Menschen. Leipzig, 1872, p. 284.

[†] Revue des Sciences Médicales. Paris, 1874, p. 385.

[‡] Les Humeurs. Paris, 1874, p. 656.

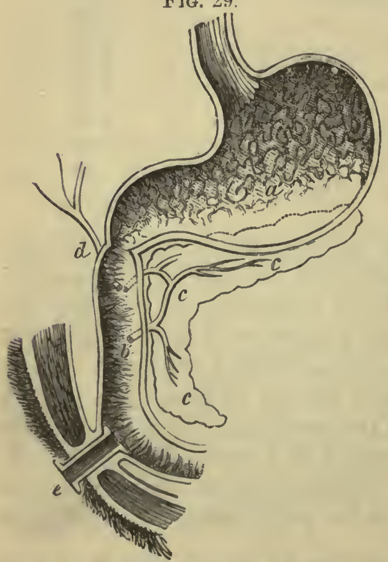
[§] Physiologische Chemie. Berlin, 1878, pp. 299, 301.

varying proportions. Generally the glycocholate may be said to preponderate in the ruminant animals, taurocholate in the carnivora. In dog's and cat's bile, the taurocholate exists alone. In human bile both substances may be present; sometimes one being the more abundant, sometimes the other. According to some writers (Robin, Hardy, Gorup-Besanez, Hoppe-Seyler) the taurocholate exists alone or in greater quantity; according to others (Bischoff, Lossen, Ranke) the glycocholate is in larger proportion. In Jacobsen's case, sodium glycocholate was invariably present, the taurocholate being less constant. We have also found human bile to contain the glycocholate without taurocholate. As the first of these substances is produced from the second, by dehydration and separation of its sulphur, it is explainable why the proportions of the two should vary from time to time.

Mode of Secretion and Discharge of the Bile.—As in man and most animals the gall-bladder forms a lateral receptacle in which the bile is wholly or partially stored up during a certain time, there are two points which require separate investigation; first, the manner and rate of its secretion by the liver; and secondly, the time and quantity of its discharge into the intestine.

In regard to its mode of secretion, the experiments of Bidder and Schmidt were performed in the following manner: They operated by tying the common bile-duct, and then opening the fundus of the gall-bladder, thus producing a biliary fistula, by which the whole of the bile was drawn off. By collecting and weighing the fluid discharged at different periods, they came to the conclusion that the secretion of bile never entirely ceases; but that it begins to increase within two and a half hours after taking food, to reach its maximum about the twelfth or fifteenth hour. Other observers have obtained different results. Arnold found the quantity largest soon after meals, decreasing again after the fourth hour. Kölliker and Müller found it largest between the sixth and eighth hours. The bile is therefore a continuous secretion, but variable in quantity at different times; being, according to the majority of observers, most abundant some hours after the commencement of digestion.

Fig. 29.



Duodenal Fistula in the Dog.—*a.* Stomach. *b.* Duodenum. *c, c, c.* Pancreas; its two ducts opening into the duodenum, one near the orifice of the biliary duct, *d*, the other a short distance lower down. *e.* Silver tube passing through the abdominal walls into the duodenum.

As to its discharge into the alimentary canal, it is certain, in the first place, that bile is present in the intestine at all times, both during digestion and in the intervals. This is shown by examination of the intestine in dogs killed at various periods after feeding. We have always found, under these circumstances, evidence of the biliary salts in the ether precipitate of the alcoholic extract of the intestinal contents, in animals killed from one to twelve days after the last meal. The biliary substances were recognized both by their solubility in water and in alcohol, their insolubility in ether, their crystalline form, and by their reaction with Pettenkofer's test. The secretion therefore continues to find its way into the alimentary canal long after the animal has been deprived of food.

But the quantity of bile passing into the intestine in a given time is much influenced by the digestive process, and its quantity is greatest soon after the commencement of digestion. We have examined this point by means of a duodenal fistula, made on the same plan as that for gastric fistulæ (Fig. 29).

To ascertain the quantity of bile discharged into the intestine, and its variations during digestion, the duodenal fluids were drawn off, for fifteen minutes at a time, at various periods after feeding, and examined as follows: each separate quantity was evaporated to dryness, its dry residue extracted with alcohol, the alcoholic solution precipitated with ether, and the ether-precipitate, representing the biliary salts present, dried, weighed, and treated with Pettenkofer's test. The result is given in the following table. At the eighteenth hour the quantity of fluid was so small that the amount of its biliary ingredients was not ascertained. It reacted, however, with Pettenkofer's test, showing that bile was present.

Discharge of Intestinal and Biliary Fluids from Duodenal Fistula in a Dog Weighing 16.5 Kilogrammes.

Time after feeding.	Quantity of fluid in 15 minutes.	Dry residue of the same.	Quantity of biliary salts.	Proportion of biliary salts in the dry residue.
	(Grammes.)	(Grammes.)	(Grammes.)	(Per cent.)
Immediately.	41.467	2.138	0.648	30
1 hour.	128.936	6.803	0.259	3
3 hours.	50.537	3.887	0.259	7
6 "	48.594	4.729	0.227	5
9 "	55.721	5.053	0.291	6
12 "	21.057	1.490	0.243	16
15 "	22.482	1.166	0.259	22
18 "	—	—	—	—
21 "	24.880	0.712	0.064	9
24 "	10.561	0.615	0.210	34
25 "	9.783	0.324	0.194	60

The bile therefore passes into the duodenum in much the largest quantity immediately after feeding. During the intervals of digestion it accumulates in the gall-bladder; and in animals which have been for some time without food the gall-bladder is usually distended with bile, while in those killed immediately or soon after feeding it is comparatively empty. At the commencement of digestion it is excited to contraction, causing a sudden flow of bile into the duodenum. After that time the discharge remains nearly constant; not varying much, in a dog of sixteen and a half kilogrammes weight, from 256 milligrammes of the biliary salts every fifteen minutes, or a little over one gramme per hour.

Daily Quantity of the Bile.—The first experiments of value on this point were those of Bidder and Schmidt,* in 1852. They were performed on dogs, cats, sheep, and rabbits, in the following manner: A ligature was first placed on the common biliary duct, an opening then made in the fundus of the gall-bladder, and the bile, discharged through this opening, received in previously weighed vessels, and its quantity determined. The animal was then killed, weighed, and carefully examined, to make sure that the biliary duct had been securely tied, and that no inflammatory alteration had taken place. The observations, which were made at different periods after feeding, occupied in each animal about two hours. The average quantity for twenty-four hours was then calculated from a comparison of the above results; the amount of solid ingredients being ascertained in each instance by evaporating a portion of the bile and weighing the dry residue.

It was found that the daily quantity varied considerably in different animals, being much greater in the herbivora than in the carnivora. The results obtained were as follows:

DAILY QUANTITY PER KILOGRAMME OF BODILY WEIGHT.

	Fresh bile.	Dry residue.
In the cat . . .	14.537 grammes.	0.816 grammes.
" dog . . .	19.956 "	0.985 "
" sheep . . .	25.372 "	1.340 "
" rabbit . . .	136.556 "	2.464 "

According to the later researches of Schiff,† these estimates are not beyond the truth, since he obtained considerably larger quantities in the dog, by a fistula of the gall-bladder, without tying the common biliary duct. While the average quantity obtained in this animal by Bidder and Schmidt was 0.832 gramme of fresh bile per hour for every kilogramme of bodily weight, in the experiments of Schiff it was 1.3 to 3.2 grammes per kilogramme per hour.

Since in man the processes of digestion and nutrition resemble those of the carnivora, rather than those of the herbivora, it is the former which should be selected as a term of comparison for estimating the daily quantity of bile. If we apply accordingly to the human subject the results obtained by Bidder and Schmidt from the cat and dog, the quantity of bile, for a man weighing 65 kilogrammes, would be a little

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* Verdauungssaefte und Stoffwechsel. Leipzig, 1852.

† Archiv für die gesammte Physiologie. Bonn, 1870, Band iii., p. 598.

over 1100 grammes per day. Ranke,* in his case of human biliary fistula, obtained a result not essentially different. The patient weighed only 47 kilogrammes; the average quantity of bile discharged in twenty-four hours being 652 grammes, the maximum 945 grammes. In a man of 65 kilogrammes' weight this would correspond, for the average, to 902 grammes, and for the maximum to 1307 grammes. The entire quantity of bile, therefore, for a man of medium size, is evidently not far from 1000 grammes per day. This contains about 30 grammes of solid ingredients.

Physiological Action of the Bile.—Notwithstanding the well-marked character of the bile, and its frequent investigation by competent observers, its physiological action remains extremely obscure. We can state only a few points, which embrace nearly the whole of our positive knowledge in regard to it.

In the first place, the bile is present in all vertebrate animals without exception, and is discharged from the biliary duct into the intestine near its upper extremity. This shows that the secretion is, in some way, of fundamental importance, and also that it has a probable connection with the digestive functions.

But if the bile be tested for its digestive influence on the alimentary substances, it does not exhibit any distinct properties in this respect. A diastatic action on starch, which was attributed to it by Wittich, has been found wanting by others, and according to Ewald is of inconstant occurrence, and never well marked in character. Its action on fatty substances is but little more characteristic. It certainly has the property of dissolving fats to some extent, both in the free form and when saponified; and such solvent power belongs also to a watery solution of the biliary salts. But 'by far the greater part of the fatty substances in digestion are absorbed in the emulsioned form, without solution or saponification; and, according to Hoppe-Seyler,† the quantity of oily matter which the bile can dissolve is far below that absorbed from the intestine. A direct emulsifying agency cannot be attributed to the bile, since, when shaken up with oil, its emulsive effect is so incomplete and temporary as to be practically without importance. It has been thought to have an indirect action in this respect, when the fats are partially acidified and saponified by the pancreatic juice, by dissolving the saponified portion, and thus facilitating the emulsion of the remainder. But emulsion takes place so instantly and completely by the contact of oil with pancreatic juice, when no bile is present, that its normal share in the process can hardly be a large one. As regards the albuminous matters, there is no evidence that the bile exerts upon them any specific action.

Another influence regarded as belonging to the bile is that of exciting the muscular action of the intestine, and thus serving as a stimulus

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* Physiologie des Menschen. Leipzig, 1872, p. 284.

† Physiologische Chemie. Berlin, 1878, p. 315.

to its peristaltic movement. It is no doubt true that torpidity of the intestine is a usual accompaniment of clay-colored evacuations from the absence of bile; and on the other hand that bile, if applied to the muscular coat of the intestine, will excite its contraction. But this cannot be regarded as fully accounting for so abundant and peculiar a secretion.

Furthermore, the bile has been thought to assist by its physical properties the absorption of oily matter by the intestine. It has been shown by direct experiment to aid the passage of oily matter through organic membranes or parchment paper; that is, oily matter will pass through these membranes more readily when they are moistened with bile than when simply wetted with water; and it is from these experiments that the supposed action of bile has been inferred. But the villi of the intestine are not simply membranes moistened with water. They are penetrated by alkaline and albuminous fluids, their blood-vessels contain an abundance of liquid organic material, and the fatty emulsion formed by the pancreatic juice is already adapted for absorption.

Lastly, the bile has been credited with an action antagonistic to the gastric juice, by which the gastric digestion is arrested, to be followed by one of a different character in the small intestine. This is based on the fact that the two secretions will precipitate with each other when mingled in a test-tube. If one or two drops of dog's bile be added to as many cubic centimetres of fresh gastric juice from the same animal, a copious yellowish-white precipitate falls down, containing the whole of the coloring matter of the bile; and when filtered, the filtered fluid passes through colorless. A similar precipitation takes place if, instead of fresh bile, a watery solution of the biliary salts be added to gastric juice. The filtered fluid retains its acid reaction, though it has lost its digestive power.

But although the biliary matters precipitate by contact with fresh gastric juice, *they do not do so with gastric juice holding peptone in solution.* We have invariably found that if gastric juice be digested for several hours at a moderate warmth with boiled white of egg, the filtered fluid, which contains an abundance of peptone, will no longer precipitate with either bile or a watery solution of the biliary salts, even in large amount. The gastric juice and bile, therefore, do not appear finally incompatible with each other in digestion, notwithstanding their reaction when artificially mingled.

The conclusion from these facts is on the whole a negative one; and it is the present belief of most physiologists that we cannot with confidence assign to the bile any direct influence in digestion. This accords essentially with the result of our own observations.

Nevertheless, there is evidence that the bile is not simply an excrementitious product, but that it takes part, in the alimentary canal, in some process essential to life. This is shown by the fact that if it be permanently diverted from the intestine by closure of the common bile-duct, and evacuated by a fistula of the gall-bladder, the animals gradually emaciate, and die with symptoms of disordered nutrition.

This experiment has been performed at least ten times by Schwann, Bidder and Schmidt,* Bernard,† and Flint,‡ the biliary fistula remaining open, and the common bile-duct, as shown by subsequent examination, permanently closed, so that no bile found its way into the intestine. The general results in these cases were alike. The animals died in most instances between the thirtieth and fortieth day after the operation. The shortest duration of life was seven days, the longest eighty days; the average thirty-six days. The symptoms were constant and progressive emaciation, to such a degree that nearly all traces of fat disappeared from the body. The loss of weight amounted, in one case, to more than two-fifths, and in another to nearly one-half that of the whole body. There was sometimes falling off of the hair, and a putrescent odor in the feces and in the breath. Notwithstanding this, the appetite remained good. Digestion was scarcely interfered with, and none of the food was discharged with the feces; but there was, in the two cases of Bidder and Schmidt, more or less abnormal discharge of flatus. There was no pain; and death took place without violent symptoms, by gradual failure of the vital powers.

It is also certain that the bile disappears during its passage through the intestine. We have found that if dogs be killed at various periods after feeding, and the upper, middle, and lower portions of the intestinal canal separately examined, the quantity of bile present diminishes from above downward. The mass of intestinal contents also grows smaller and more consistent toward the ileo-cæcal valve; their color at the same time changing from light yellow to dark bronze or blackish-green, always strongly pronounced in the last quarter of the small intestine. The ether precipitate of their alcoholic extract, representing the biliary salts, is only one-fifth or one-sixth as abundant, in proportion to the entire solid contents, in the large intestine as in the small; and if dissolved in water, that from both upper and lower portions of the small intestine always gives Pettenkofer's reaction in less than a minute and a half, while in that from the large intestine no red or purple color is usually produced, even at the end of three hours. Bidder and Schmidt§ analyzed all the feces passed during five days by a healthy dog weighing 8 kilogrammes. From the result of former experiments (page 182) it is known that a dog of this size must have secreted during that time not far from 40 grammes of solid biliary matter; while the entire quantity of these matters in the feces was less than 4 grammes. The acids of the biliary salts have been found by Hoppe-Seyler in the feces, both of the dog and the calf; but according to his own estimate‖ their quantity, as discharged with the excrement, is always insignificant in proportion to that secreted in a corresponding time.

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* Verdauungssaefte und Stoffwechsel. Leipzig, 1852, p. 103.

† Liquides de l'Organisme. Paris, 1859, tome ii., p. 199.

‡ Physiology of Man. New York, 1867, p. 369.

§ Verdauungssaefte und Stoffwechsel. Leipzig, 1852, p. 217.

‖ Physiologische Chemie. Berlin, 1878, p. 337.

The biliary matters, therefore, are either so decomposed in the intestine as to lose their distinctive reactions, or they are reabsorbed in some form by the mucous membrane, and again introduced into the circulation. It seems highly probable that they are reabsorbed. In the experiments of Bidder and Schmidt, above quoted, this point was examined by elementary analysis of the fecal ingredients. In dog's bile the only or preponderating biliary salt is the taurocholate, which contains sulphur. If the taurocholate had been simply decomposed or transformed in the intestine, so as to be undistinguishable by Pettenkofer's test, its sulphur ingredient would still be found in the feces. But in the animal subjected to experiment, the sulphur ingredient of the bile secreted during five days would amount to 2.364 grammes; while only 0.385 gramme of sulphur was contained in the feces for the same time, and of this only 0.155 gramme could have been derived from biliary substances. That is, not more than one-fifteenth part of the sulphur originally present in the bile could be detected in the feces.

A further evidence of the reabsorption of biliary matters from the intestine is furnished by the experiments of Schiff,* which were conducted on a different plan. This observer found that, under ordinary conditions, less pressure is required to make a fluid pass from the hepatic duct into the gall-bladder than to force it into the intestine. Unless, therefore, the pressure in the gall-bladder be increased, either by distention or by muscular contraction, it passes into the gall-bladder more readily than into the intestine; and a cystic fistula, if kept freely open, will be sufficient to discharge externally nearly all the secreted bile. Schiff demonstrated this by establishing in the same animal a fistula of the gall-bladder and one of the duodenum. So long as the cystic fistula remained open no biliary matters, or only insignificant traces of them, could be found in the duodenum.

On the other hand, when the cystic fistula was closed, the bile passed through the common duct into the intestine, thus maintaining the animal in a healthy condition. At any time, by opening the fistula and emptying the gall-bladder, the rate of secretion might be ascertained.

Schiff's observations show that by leaving open the fistula, and thus diverting the bile from the intestine, its rate of secretion is at once diminished; so that at the end of twenty-four hours, if the influence of digestion be eliminated, it is reduced to a minimum, which afterward continues with only insignificant fluctuations. But if the fistula be closed for some hours, the quantity of bile again rises to its normal standard.

The same observer obtained similar results by making, in the dog, a duodenal fistula, through which a canula was introduced into the common bile-duct. The canula had a lateral opening near its end, which might be left open or closed by shifting the position of an inner tube

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* Archiv für die gesammte Physiologie. Bonn, 1870, p. 598.

fitting closely in its cavity. Thus the bile might be either discharged externally from the orifice of the canula, or allowed to pass into the duodenum by its lateral opening. It was found that, after being discharged externally for two or three hours, its rate of secretion was much less than if it had been allowed to pass into the intestine. The results, in a dog weighing 12 kilogrammes, were as follows:

CUBIC CENTIMETRES OF BILE OBTAINED IN TEN MINUTES AFTER HAVING BEEN, FOR TWO OR THREE HOURS,

	Evacuated externally.	Discharged into the duodenum.
	2.2	6.0
	2.3	5.4
	2.1	5.6
	2.0	6.2
	1.8	6.5
	1.9	5.7
Average .	2.05	5.90

Thus the quantity of bile secreted, when allowed to follow its natural course, is nearly three times as great as when it is evacuated externally. It cannot be assumed from this that the biliary ingredients are returned directly to the liver, and again discharged with the bile; but it is difficult to avoid the conclusion that its ingredients are absorbed from the intestine, and supply in some way the materials for continued secretion.

Finally, Tappeiner* has detected the biliary salts, by Pettenkofer's test, in chyle from the thoracic duct. With 150 cubic centimetres of chyle, taken from the duct two hours after feeding, in a dog weighing 8 kilogrammes, he obtained a complete biliary reaction by the above test.

As a rule, however, the biliary salts appear to undergo, before absorption, some change which modifies their original properties; and attempts to distinguish them in the blood of the portal vein have constantly met with a negative result. The most appropriate method for such an investigation is to collect the portal blood immediately after killing the animal by section of the medulla, coagulate it by the gradual addition of alcohol, or by boiling with water and sodium sulphate in excess, evaporate it to dryness, extract the dry residue with absolute alcohol, and precipitate the filtered alcoholic solution by ether in excess. The ether precipitate is then dissolved in water, and subjected to Pettenkofer's test.

We have examined the portal blood, by this method, in the dog, one, four, six, nine, eleven and a half, twelve, and twenty-four hours after feeding. The result shows that in the venous blood, both of the portal vein and of the general circulation, there is a substance soluble in water and in alcohol, and precipitable by ether from its alcoholic solution.

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* Sitzungsberichte der Akademie der Wissenschaften. Wien, 1878. Band lxxvii. Abth. iii., p. 286.

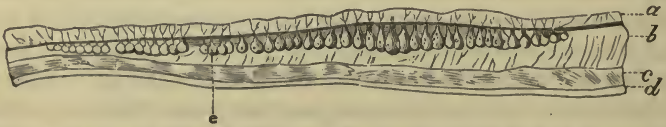
This substance is often considerably more abundant in the portal blood than in that taken from the general venous system. It resembles the biliary matters in consistency, and dissolves, like them, with great readiness in water; but in no instance have we obtained from it a characteristic reaction with Pettenkofer's test. This is not because the reaction is masked by other ingredients of the blood; for if, at the same time, bile be added to blood taken from the abdominal vena cava, in the proportion of one drop of bile to seven or eight cubic centimetres of blood, and the two specimens treated alike, the ether-precipitate may be considerably more abundant in the case of the portal blood; and yet that from the blood of the vena cava, dissolved in water, will give Pettenkofer's reaction perfectly, while that of the portal blood will yield no such reaction.

The bile, accordingly, is a secretion which has not yet accomplished its function when secreted and poured into the intestine. Although its most abundant discharge coincides with the beginning of digestion, it does not seem to aid the operation of the digestive fluids, but rather to be itself acted on by them, and converted into other forms of combination. The intestine is, therefore, for the biliary ingredients, a place of passage, where they undergo an intermediate transformation between their production in the liver and their final disappearance in other parts. It is still unknown what new substances are produced by these changes; but they seem to be essential for general nutrition, which cannot be long maintained if the biliary matters are permanently withdrawn from the system.

Intestinal Juice.

The secretory apparatus of the small intestine consists of two sets of glandular organs; first, *Brunner's glands*, which are lobulated glandules, confined to the upper part of the duodenum, for a distance of several centimetres from the pylorus; and, secondly, the *follicles of Lieberkühn*, which are simple tubular glandules, occupying the substance of the mucous membrane for the whole length of the small intestine.

FIG. 30.

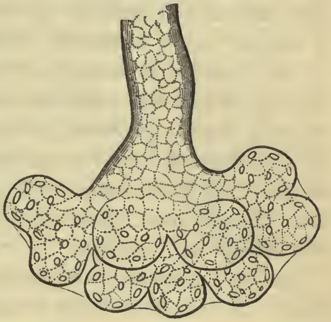


LONGITUDINAL SECTION OF WALL OF DUODENUM IN THE DOG; showing the submucous layer of Brunner's Glands.—*a*. Mucous membrane. *b*. Layer of submucous connective tissue, in which the glands are situated. *c*. Muscular coat. *d*. Peritoneal coat. *e*. Brunner's glands, with their ducts opening on the free surface of the mucous membrane. (Bernard.)

Brunner's glands, or the duodenal glandules, are situated in the submucous layer of connective tissue in the duodenum. They are spherical, or, when thickly set, irregularly polygonal in shape from mutual pressure, and from $\frac{1}{2}$ to 1 millimetre in diameter.

In structure, they resemble the lobulated glandules of the mouth, being composed of rounded follicles clustered about a central excretory duct. Each follicle is about $\frac{1}{10}$ of a millimetre in diameter, and consists of a membranous wall, lined with nucleated cells of glandular epithelium. The follicles collected round each terminal branch of the duct are bound together by a thin layer of connective tissue, and covered with a plexus of capillary blood-vessels.

Fig. 31.

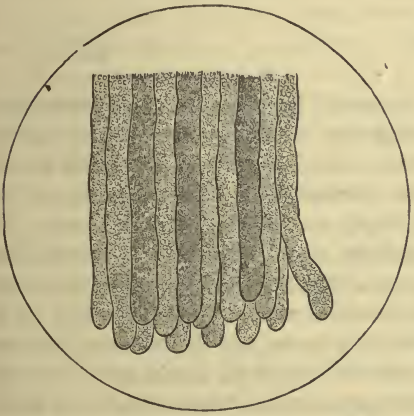


Portion of one of **Brunner's Glands**; from human intestine.

The follicles of Lieberkühn, which are much more numerous than the preceding, occupy the entire thickness of the mucous membrane. They are nearly straight tubules, from $\frac{1}{12}$ to $\frac{1}{16}$ of a millimetre in diameter, lined with cylindrical epithelium, opening on the free surface of the mucous membrane, and terminating below by rounded extremities. They are so thickly set that, for the most part, there appears to be no space between them, except that occupied by capillary blood-vessels.

The fluid produced by the mucous membrane of the small intestine consists of the secretions of these two sets of glands. But owing to the situation of Brunner's glands, their secretion is always mixed with other fluids; and by the intestinal juice proper is understood the secretion of Lieberkühn's follicles. It is by no means easy to obtain this fluid in pure form and normal condition. The follicles have no single excretory duct, in which a canula might be inserted; and a fistulous opening in the intestine would yield a mixture of all the secretions discharged into its cavity. If these should be shut off by a ligature applied above the fistula, the disturbance of the digestive process would be so great, that the experiment could hardly be expected to give valuable results.

Fig. 32.



Follicles of Lieberkühn; from small intestine of dog.

Nevertheless, attempts have been made, by various methods, to obtain the intestinal juice for examination. Bidder and Schmidt tied the biliary and pancreatic ducts, and then established an intestinal fistula below, from which they extracted the fluids accumulated in the gut. Frerichs operated by opening the abdomen, taking out a loop of intestine, emptying it so far as possible by gentle pressure, isolating its cavity by the application of two ligatures 15 or 20 centimetres apart, and returning it to the abdominal cavity. After a few hours the animal was killed, and the fluid, which had collected in the isolated portion of the intestine, taken out and examined. Colin adopted a similar method, in the horse, with greater precautions. While digestion was in full activity he took out, through an opening in the flank, a loop of small intestine, which he isolated by two compressors, made of flat wooden or metallic strips, enveloped by velvet ribbon, and fastened in such a way that the inner surfaces of the intestine were retained in close contact, without bruising their tissues. The compressors being applied from one to two metres apart after the included portion of intestine had been emptied by gentle pressure, the whole was returned into the abdomen, the wound closed by sutures, and the animal killed at the end of half an hour.

On the average, 100 grammes of fluid had accumulated within this time. It was clear, with a slightly yellowish or amber tint, alkaline in reaction, and with a specific gravity of 1010. According to the analysis of Lassaigne, it was composed as follows:

COMPOSITION OF INTESTINAL JUICE FROM THE HORSE.

Water	981.0
Albuminous matter	4.5
Sodium chloride Potassium chloride Sodium phosphate Sodium carbonate	14.5
	1000.0

Thiry separated a portion of the small intestine from the remainder by two transverse sections, leaving the mesentery and vessels of the isolated portion uninjured, and then united by sutures the divided ends of the remaining portions, so as to reëstablish the continuity of the intestine, but with a portion, 10 or 15 centimetres long, left out. Of this isolated portion, still nourished by its blood-vessels, he closed one end by sutures, so as to make of it a blind extremity, while the other he fastened to the edges of the external wound in such a way as to make a permanent fistula. When the parts had healed, and natural digestion was reëstablished, he collected the fluid discharged from the isolated portion of intestine. This operation has been repeated by other observers. The objection to it is that the isolated portion of intestine, after being for some weeks precluded from taking part in the process of digestion, becomes partially atrophied, and cannot be relied on as furnishing a secretion similar to the normal intestinal juice. The results obtained vary, some of them indicating that the secretion converts starch into sugar, and has a dissolving action on coagulated albuminous matters, others that these properties are absent or but slightly developed. Colin found that the fluid obtained from the horse by his method had the power of slowly transforming starch-paste into glucose, and that it could emulsify oily substances with considerable energy. Bernard found the same properties in a fluid obtained from the dog, by opening the small intestine after some days' fasting. But on the whole these results have not been very satisfactory, owing to the doubt how far the fluids obtained represent the normal secretion of the intestine.

Furthermore, two instances of intestinal fistula have been observed in man. In the case examined by Busch,* the patient, a woman, 31 years of age, had been gored by a steer; causing a fistulous opening in the abdominal wall, midway between the umbilicus and the pubis. It communicated with the small intestine very near its upper extremity, the two portions of intestine being completely separated from each other at the fistula. The portion of intestine below the fistula, accordingly, contained none of the fluids from above, but only its own secretion. Busch operated by introducing into the lower portion of the intestine various alimentary substances, and ascertaining how far they were liquefied and absorbed. He concluded that there was a perceptible, but not very energetic, solvent action on albuminous matters, a much stronger one on starchy substances, and either very little or none at all on fat.

The case of Demant† was somewhat similar, except that the fistulous separation between the two portions of small intestine was near its lower instead of its upper extremity. It was the result of an operation for strangulated hernia in a man forty-two years of age, and at the time of the observation in good health and condition. Demant collected the fluids secreted by the lower portion of the intestine, and experimented with them on different kinds of food by artificial digestion at the temperature of 36° to 38° C. He found the intestinal juice very scanty, exuding from the fistula usually in drops. The largest quantity obtained was 25 cubic centimetres per day; the average from 15 to 20 cubic centimetres. It was a thin, clear, alkaline fluid, not coagulable by heat, but precipitable by acetic acid owing to its mucous ingredients. It contained no pepsine ferment, had no transforming action on albuminous matters, and produced no peptone from coagulated fibrine, even after a digestion of twelve hours. It slowly transformed starch paste into glucose, requiring five hours' time for that purpose. Oily matters, containing free fatty acid, were emulsioned by it, but it had no perceptible effect on neutral fats.

From these observations it appears that the intestinal juice cannot be an abundant secretion, nor a very active agent in the digestive process. It is an alkaline fluid, with a moderate transforming action on starchy matters, much inferior to that of the pancreatic juice. Its

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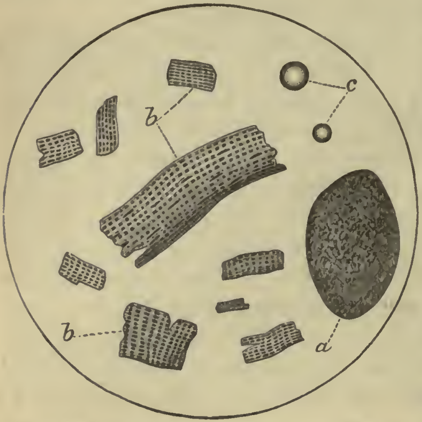
* Archiv für pathologische Anatomie und Physiologie. Berlin, 1858, Band xiv., p. 140.

† Archiv für pathologische Anatomie und Physiologie. Berlin, 1879, Band lxxv., p. 419.

emulsifying action on fats is also quite secondary in importance, and its power of digesting albumenoid substances doubtful or imperfect. Its most important property is perhaps the simple one of lubricating the mucous membrane, and facilitating the passage of alimentary materials through the intestine.

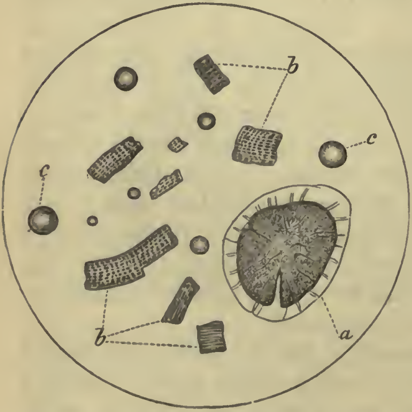
Fig. 33.



Contents of Stomach during Digestion of Meat, from the Dog.—*a.* Fat Vesicle, filled with opaque, solid, granular fat. *b*, *b*. Partially disintegrated muscular fibre. *c.* Oil globules.

Digestion in the Intestine.—The digestive process, which commences in the stomach under the influence of the gastric juice, is continued and completed during the passage of the food through the small intestine. Its details may be examined in successive parts of the alimentary canal, in animals killed while digestion is going on. After a meal, consisting of muscular flesh and adipose tissue, the stomach contains (Fig. 33) masses of softened meat, smeared with gastric juice, and a moderate quantity of grayish grumous fluid with an acid reaction. This fluid contains isolated muscular fibres, more or less reduced to fragments. The fat vesicles of beef are but little altered, and there are only a few free oil globules in the mixed fluids of the stomach. In the duodenum the muscular fibres

Fig. 34.



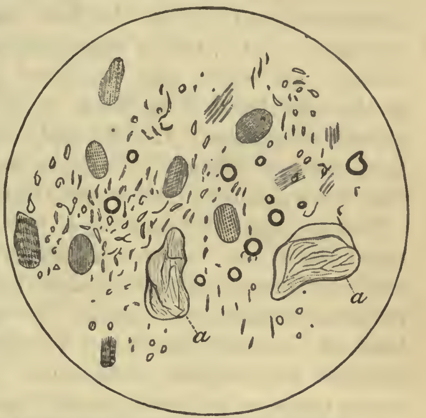
From Duodenum of Dog during Digestion of Meat.—*a.* Fat vesicle, with its contents diminishing. The vesicle is beginning to shrivel and the fat breaking up. *b*, *b*. Disintegrated muscular fibre. *c*, *c*. Oil globules.

Fig. 35.

From Middle of Small Intestine.—*a*, *a*. Fat vesicles, nearly emptied of their contents.

are further disintegrated (Fig. 34). They are much broken up, pale, and transparent, but can still be recognized by their characteristic markings and striations. The fat vesicles also become altered in the duodenum. The solid granular fat of beef becomes liquefied and emulsioned; and appears under the form of free oil drops and fatty molecules; while the fat vesicle is partially emptied, and more or less collapsed. In the middle and lower parts of the small intestine (Figs. 35 and 36) these changes continue. The muscular fibres become more disintegrated, producing a large quantity of granular debris, which is at last dissolved. The fat also progressively disappears, and the vesicles may be seen in the lower part of the intestine completely collapsed and empty.

Fig. 36.



From Last Quarter of Small Intestine.—*a*, *a*. Fat vesicles, quite empty and shrivelled.

In this way the digestion of the food goes on continuously throughout the small intestine. At the same time it results in the production of three different substances, namely: 1st. Peptone, from the digestion of albuminous matters; 2d. Chyle, from the emulsion of the fats; and 3d. Glucose, produced by the transformation of starch. These substances are then ready to be taken into the circulation; and as the mingled intestinal contents pass successively downward, the products of digestion, together with the digestive secretions, are absorbed by the mucous membrane and carried away by the blood-vessels.

The Large Intestine and its Contents.

The mucous membrane of the large intestine is provided with tubular follicles not essentially different in their anatomical characters from the follicles of Lieberkühn. Their secretion, however, appears to be scanty. According to Ranke, fistulous openings in the large intestine do not yield any notable quantity of fluid, and if a loop of the gut be isolated by ligatures, an accumulation of mucus-like matter is the only result. In the rabbit, after ligature of the vermiform appendix, Funke obtained, at the end of from two to four hours, a quantity of turbid alkaline secretion with which the appendix had become filled. This fluid was without action on coagulated albumen; but it transformed starch into sugar, and also decomposed the sugar with production of lactic and butyric acids. The same change was produced on starch introduced into the cavity of the appendix.* This accounts for the acid reaction sometimes found

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* Ranke, Physiologie des Menschen. Leipzig, 1872, p. 297.

in the cæcum of herbivorous animals, although the mucous surface of the large intestine is constantly alkaline.

As the remnants of the alimentary mass pass the ileo-cæcal valve into the large intestine, they acquire a pasty consistency and a repulsive odor. Both these changes become more marked in the middle and lower part of the gut, until all the superfluous fluids have disappeared, and the consistency and odor of the feces are fully developed. This is not a putrefactive odor, but is characteristic of the contents of the large intestine. Its source may be either a peculiar transformation of some of the ingredients of the food, or an excretory action of the intestinal mucous membrane. It is probably in great part the result of an excretion, since in different animals, whatever the nature of their food, the feces have usually a distinct odor characteristic of the species.

The average daily quantity of feces in man is 150 grammes, of which about 75 per cent. is water and 25 per cent. solid residue. They consist, first, of undigested remnants of the food, and secondly, of excreted material from the alimentary canal. The undigested substances derived from the food are mainly animal or vegetable tissues, which, from their constitution, are incapable of digestion. These are elastic fibres, or bits of elastic tissue, which nearly always pass the intestine unchanged; shreds of tendon or fascia not sufficiently softened by cooking; horny epidermic tissues, both animal and vegetable; and the spiral tubes and ducts of vegetable substances. The excreted materials are the mucus of the large intestine and probably also the volatile substances which produce the fecal odor. The coloring matters of the bile are present in a more or less altered form.

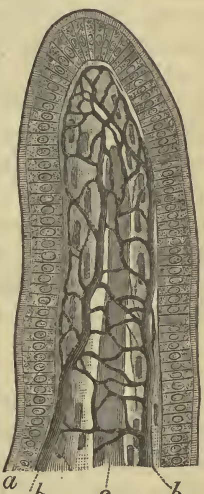
The mineral salts in the feces amount to a little over one-tenth of the solid ingredients. They are for the most part the same with those of the animal fluids in general, but are mingled in different proportions; only about 4 per cent. consisting of the soluble chlorides and sulphates, while fully 80 per cent. are composed of lime and magnesium phosphates. They are regarded as derived partly from the unabsorbed mineral ingredients of the food, and partly from the intestinal secretions.

CHAPTER II.

ABSORPTION.

THE absorption of the digested food, which is the main office performed by the small intestine, is provided for by a special structure of its mucous membrane. The apparatus consists in an abundance of minute eminences or prolongations, the so-called *villi* of the small intestine, so closely set over its surface as to give it a characteristic velvety appearance. They are found throughout this part of the alimentary canal, from the pylorus to the free border of the ileo-cæcal valve, most abundant in the duodenum and jejunum, rather less so in the ileum, but averaging in number from 20 to 40 to the square millimetre. In the upper part of the intestine they are flattened and leaf-life, cylindrical or filamentous in its middle and lower portions In man they are about one-half a millimetre in length.

Fig. 37.



An Intestinal Villus. *a.* Layer of cylindrical epithelium, with its external transparent striated portion. *b, b.* Blood-vessels entering and leaving the villus. *c.* Lymphatic vessel occupying its central axis. (Leydig.)

Each villus is covered with nucleated, finely granular cylindrical epithelium cells, closely united with each other by their lateral surfaces, and presenting at their outermost portion a transparent layer, marked, according to Kölliker, Frey, and other observers, by fine vertical striations. It is penetrated below by blood-vessels from a terminal twig of the mesenteric artery, which form by their division and inosculation a capillary net-work beneath the epithelial layer. At its base they reunite to form a venous branch, one of the rootlets of the mesenteric vein.

In the deeper part of the villus, and nearly in its longitudinal axis, there is the commencement of a lymphatic vessel, which, after its emergence, joins the general abdominal system of lymphatic or lacteal vessels. It is usually single in the filiform and cylindrical villi, double or triple in those of more flattened form. It has exceedingly thin walls, consisting of a single layer of flattened epithelium cells.

Closed Follicles of the Small Intestine.—In addition to the follicles of Lieberkühn, the intestine presents two sets of glandular-looking organs, known as the *glandulæ solitariæ* and the *glandulæ agminatæ.* The first of these, or the solitary glandules, are found in the upper part of the intestine, scattered over its surface, as minute whitish points. Farther down they occur in clusters of several together, and in the lower part of the jejunum and in the ileum they constitute rounded or oval patches, from $1\frac{1}{2}$ to 5 centimetres in length, known as "Peyer's patches." These patches are situated opposite the attachment of the mesentery, with their long diameter parallel to the axis of the intestine.

The structure of the solitary glandules and of those forming Peyer's patches is the same.

Each follicle is a rounded or ovoid body, from one-half to two millimetres in diameter, situated partly in the mucous membrane and partly below it. It consists of a closed capsule, from the inner surface of which slender anastomosing filaments pass through the substance of the organ, forming a scaffolding or frame-work of minute fibres. In the interstices there is a small quantity of fluid, together with an abundance of *lymph corpuscles*, or faintly granular cells about 13 mmm. in diameter. The follicle is also provided with capillary blood-vessels, which penetrate its investing capsule, inosculate freely in its interior, and return upon themselves in loops near its centre.

These follicles have a close relation with the lymphatics of the intestine. The lymphatic vessels coming from the villi form a plexus in the substance of the mucous membrane, from which branches pass to the follicles and ramify over them, forming another plexus upon their investing capsule. They do not, however, penetrate into the interior of the follicles, which are occupied by blood-vessels alone. Owing to the analogy in structure between these bodies and portions of the lymphatic glands, as well as to the fact that the lacteals from the neighborhood of Peyer's patches are more numerous than those from other points of the intestine, the closed follicles are generally regarded as belonging to the system of the lymphatic glands. They furnish no secretion to the intestinal cavity, but are connected in some way with the elaboration of the absorbed materials.

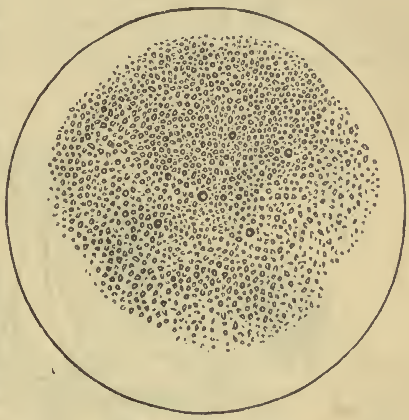
Absorption by the Villi.

The villi are the active agents in the process of absorption. The entire mucous membrane of the small intestine, including the valvulæ conniventes, represents about 6000 square centimetres of surface; and as the number of the villi is, on the average, not less than 30 to the square millimetre, there must be at least from fifteen to twenty millions of them in the intestine. By their abundance, as well as by their projecting form, they multiply the extent of contact of the digested fluids with the mucous membrane, and increase, to a corresponding degree, the activity of absorption. They hang out into the nutritious, semifluid mass in the intestinal cavity, as the roots of a tree penetrate the soil; and they imbibe its liquefied portions with a rapidity which is in proportion to their extent of surface and the movement of the circulation.

Absorption is also hastened by the peristaltic action of the intestine.

The muscular layer throughout the alimentary canal is double, consisting of circular and longitudinal fibres. Their action may be excited in the recently killed animal, by pinching the exposed intestine with the blades of a forceps. A contraction takes place at the spot irritated, the intestine is reduced in diameter, and its contents forced onward. The local contraction then propagates itself to the neighboring parts, while the portion originally contracted becomes relaxed; and a slow, continuous, creeping motion of the intestine is produced, by successive waves of contraction and relaxation, following each other from above downward. At the same time the longitudinal fibres have a similar alternate action, drawing the narrowed portions of intestine up and down, as they successively become contracted or relaxed. The effect produced is a peculiar, writhing, worm-like, or "vermicular" motion, among the coils of intestine. During life, this action of the intestine is excited by the food undergoing digestion. By its means the substances passing from the stomach into the duodenum are made to traverse the entire length of the small intestine, and brought in contact successively with the whole of its mucous membrane. During this passage the absorption of the digested food takes place, so that its liquefied portions disappear, and, at the lower end of the small intestine, there remains only the undigested part of the food, together with the refuse of the intestinal secretions. These pass through the ileo-cæcal orifice into the large intestine, and are there reduced to the condition of feces.

Fig. 38.



Chyle from Commencement of Thoracic Duct; from the Dog.

The fluids of the intestine are first absorbed by the epithelial cells of the villi, and thence transmitted to the deeper portions of the tissue. This passage of the products of digestion through the substance of the epithelial cells is difficult of demonstration for homogeneous liquids, but it may be seen in the fatty matters of the chyle. Chyle, drawn either from the lacteal vessels or from the thoracic duct, presents the same appearance, containing fatty matter under the form of granules, which vary in size from 2.5 mmm. downward, and which have the usual characters of oil in a state of minute subdivision.

The emulsioned fat of the chyle has accordingly passed from the cavity of the intestine into that of the lacteal vessels. Its transmission is facilitated by the alkaline condition of the blood and of the intestinal juices. Oil by itself is non-diffusible. If a fluid containing oil be placed on one side of an animal membrane, and pure water on the other, the water will readily penetrate the substance of the membrane, while the oily particles cannot be made to pass under any ordinary pressure. But though this be true for pure water, it is not true for slightly alkaline fluids like the serum of blood or the lymph. This was shown by the experiments of Matteucci, with an oily emulsion in an alkaline fluid containing 4.3 parts of potassium hydrate per thousand. Such a solution has no alkaline taste, and its action on reddened litmus-paper is about equal to that of the lymph and chyle. If such an emulsion be placed in an endosmometer, together with a watery alkaline solution of similar strength, the oily particles penetrate the animal membrane without much difficulty, and mingle with the exterior fluid. Endosmosis will therefore take place with a fatty emulsion, provided the fluids be slightly alkaline in reaction.

When the molecules of the chyle are taken up by the villi, their passage into and through the epithelial layer produces a marked alteration in the appearance of its cells. In the intervals of digestion these cells are nearly transparent and homogeneous-looking, presenting under the microscope the appearance of a very delicate granulation. (Fig. 39.) But during the digestion and absorption of fatty matters, their substance is crowded with oily particles. (Fig. 40.) The oily matter then passes onward, penetrating deeper into the substance of the villus, until received by the capillary vessels in its interior.

Fig. 39.

Intestinal Epithelium; from the Dog while fasting.

Fig. 40.

Intestinal Epithelium; from the Dog during the digestion of fat.

Absorption by the Blood-vessels.—The final absorption of the digested fluids is accomplished mainly by the blood-vessels of the intestinal villi. Their situation, their numbers, and the rapid movement of the blood, are all favorable conditions for the performance of this function. The capillary plexus of each villus is situated in its superficial part, immediately beneath the epithelium cells, so that the absorbed fluids, after passing through the epithelial layer, come at once in contact with the vascular network. The extension of absorbing surface, from the division and inosculation of these vessels, and the renovation of their fluids by the movement of the circulation, provide for their constant activity, and drain away the absorbed fluids from the interior of the villus as fast as they are taken up by its surface.

The activity of the blood-vessels in this process is a matter of direct observation. It was first shown by Magendie,* who found that the absorption of poisonous substances would take place, in the living animal, both from the cavity of the intestine and from the tissues of the leg, notwithstanding that all communication through the lacteals and lymphatics was cut off, and the blood-vessels alone remained. These results were corroborated by Panizza, who succeeded in detecting the substances absorbed in the venous blood returning from the part. This observer, after having opened the abdomen of a horse, drew out a fold of the small intestine, about 20 centimetres in length, which he included between two ligatures. A ligature was then placed upon the mesenteric vein receiving the blood from this portion of intestine; and, in order that the circulation might not be interrupted, an opening was made in the vein behind the ligature, so that the blood brought by the mesenteric artery, after circulating in the intestinal capillaries, passed out at the opening, and was collected for examination. Hydrocyanic acid was then introduced into the intestine, and almost immediately afterward its presence was detected in the blood flowing from the venous orifice. The animal, however, was not poisoned, since the acid was prevented by the ligature from gaining an entrance into the general circulation.

Fig. 41.

Capillary Blood-Vessels of the Intestinal Villi; from the Mouse. (Kölliker.)

Panizza afterward varied this experiment in the following manner: Instead of tying the mesenteric vein, he simply compressed it. Hydrocyanic acid being then introduced into the intestine, no effect was produced so long as the vein remained compressed; but as soon as the

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* Journal de Physiologie. Paris, 1825, tome i., p. 18.

blood was again allowed to pass, symptoms of general poisoning were manifest. Lastly, in a third experiment, he removed the nerves and lacteal vessels supplying the intestinal fold, leaving the blood-vessels untouched. Hydrocyanic acid, introduced into the intestine, found an immediate entrance into the general circulation, and the animal was at once poisoned. The blood-vessels, therefore, are not only capable of absorbing fluids from the intestine, but may take them up even more rapidly than the lacteals.

The entrance of digested materials into the blood-vessels of the intestine is demonstrated in a similar way. After the digestion of food containing albuminous and starchy ingredients, both glucose and peptone are met with in the blood of the portal vein. Emulsioned fatty matters may also be followed, in their passage through the same channels, by the chylous aspect which they communicate to the portal blood. The blood of the portal system, in carnivorous animals, during digestion, contains fatty matter in a state of minute subdivision, similar in appearance to that found in the chyle and in the villi; and these ingredients are often so abundant as to cause a turbid appearance in the serum after coagulation. A variety of observers (Lehmann, Schultz, Simon), in examining the blood from different parts of the body, have also found the blood of the portal system considerably richer in fat than that of the arteries or of other veins, particularly while digestion is going on.

Absorption by the Lacteals.—The absorption of digested materials, particularly of the fatty matters, is also accomplished by the lacteals of the small intestine. These vessels are part of the great lymphatic system, which is distributed everywhere in the integuments of the head, the parietes of the trunk, the limbs, and in the glands, muscles, and mucous membranes throughout the body. Originating in the tissues of these organs, they pass from the periphery toward the centre, converging and uniting with each other like the veins, and passing, at various points, through the lymphatic glands.

The fluid generally contained in these vessels is the "lymph." It is a colorless or slightly yellowish transparent liquid, absorbed by the lymphatic vessels from the various tissues, and containing, beside water and saline matters, a small quantity of fibrine and albumen.

The lymphatic vessels of the intestine originate in the villi, as longitudinal spaces lined with flattened epithelium cells, becoming provided, after a short distance, with transparent, elastic coats, like those of the capillary blood-vessels. On emerging from the villi they become part of the lymphatic plexus, from which the main branches pass between the layers of the mesentery, from the intestine toward the posterior part of the abdomen. In this part of their course they inosculate with each other by transverse branches, and pass through several ranges of mesenteric glands, representing the lymphatic glands of the abdominal cavity. Near the attached portion of the mesentery, on the right side of the abdomen, about the level of the second lumbar vertebra, they terminate in a saccular dilatation, the "receptaculum chyli." From this point the thoracic duct passes upward through the chest, crossing obliquely from right to left, and terminating in the left subclavian vein, at its junction with the jugular of the same side.

In the intervals of digestion the fluid contained in the lymphatic vessels is everywhere the same in appearance. Its colorless and transparent character, the small size of the vessels, and the thinness and delicacy of their coats, make them nearly or quite invisible to the unaided eye. But during the absorption of food the lymphatics of the small intestine are distended with chyle, and thus become visible as opaque white filaments, ramifying in the intestinal walls, converging from the intestine to the receptaculum chyli, and contrasting strongly with the semi-transparent ruddy color of the neighboring tissues. Owing to the appearance thus given to the vessels by the milky fluid which they contain, they have received the name of the *lacteals*, or lactiferous vessels of the abdomen.

The presence of chyle in the lacteals is, therefore, only periodical. The fatty substances begin to be absorbed during digestion, as soon as they have been emulsioned by the digestive fluids. As the process goes on, they accumulate in larger quantity, and gradually fill the whole lacteal system of the abdomen. But as digestion and absorption come to an end, the milky fluid disappears from these vessels, and they resume their former transparent appearance.

The lacteals, accordingly, are the lymphatics of the small intestine, which, in addition to the lymph which they usually contain, have absorbed a fluid rich in emulsioned fat. They are then distinguished from the lymphatics elsewhere by the milky character of their contents, which accumulate in the receptaculum chyli, and may be followed thence through the thoracic duct, to its termination in the subclavian vein. (Fig. 42.)

Fig. 42.

Lacteals and Lymphatics, during digestion.

It was owing to the opacity of the lacteals during digestion that these vessels were discovered in 1622 by Asellius, who first saw them on opening the abdomen of a dog, a few hours after the ingestion of food. The discovery of the general lymphatic system was made subsequently by Rudbeck and Bartholin, in 1651 and 1653, and was consequent upon the previous observations on the lacteals of the abdomen.

That the white color of the chyle during digestion is really due to the presence of fatty substances absorbed from the intestine, is shown by the fact that its intensity is in proportion to the quantity of fat in the food. It is generally less marked in herbivorous than in carnivorous animals. According to the observations of Tiedemann and Gmelin, in a dog fed with fatty matters the lacteals are abundantly filled with an opaque white fluid, while in the same animal fed with starchy matters alone, the chyle is pale and but slightly opaline; and Bernard has shown that if, in a dog after several days' fasting, a little ether, containing fat in solution, be injected into the stomach, without the introduction of other food, at the end of a few hours the lacteals are fully distended with chyle, similar in appearance to that seen during ordinary digestion.

Passage of Absorbed Materials into the General Circulation.

The products of digestion, taken up by the blood-vessels and lymphatics of the intestine, pass by two different routes into the general circulation. The blood of the portal vein, containing peptone, glucose, and molecular fat, is carried to the liver, where it traverses the capillary vessels of this organ before reaching the vena cava and the right side of the heart. The chyle, on the other hand, containing a large proportion of fatty ingredients, passes by the thoracic duct to the left subclavian vein, and there mingles with the returning current of the venous blood. But all these substances, after entering the circulation and coming in contact with the blood, are so modified as no longer to be recognizable in their original form. This change takes place very rapidly with peptone and glucose. Peptone passes, in all probability, into the condition of albumen; while the glucose is for the most part deposited in the liver in an insoluble form, those portions which reach the general circulation being decomposed or transformed, and thus losing their characteristic properties. The fatty matters also undergo a transformation while passing through the lungs by which their distinctive characters are destroyed, and they are no longer visible as oleaginous particles. This alteration is so complete, during the early part of digestion, or when the proportion of fat in the food is small, that all the oleaginous matter disappears in the lungs, and none is to be detected in the general circulation.

But as digestion proceeds, especially with food abundant in oleaginous substances, an increasing quantity of fat finds its way into the blood, and a time arrives when the whole of it is not destroyed during its passage through the lungs. Its absorption then taking place more rapidly than its decomposition, it begins to appear, in moderate quantity, in the general circulation; and, lastly, when absorption is at the point of greatest activity, it is found in considerable abundance throughout the vascular system. At this period, some hours after the ingestion of food rich in oleaginous matters, the blood, not only of the portal vein, but also of the general circulation, contains a superabundance of molecular fat, derived from the digestive process. Blood drawn at that time, from the veins or the arteries in any part of the body, will present the appearance known as that of "chylous" or "milky" blood. On the separation of the clot the serum is turbid; and after a few hours of repose, its fatty ingredients rise to the surface in an opaque, creamy-looking pellicle. This appearance has been sometimes observed in human blood, in cases of sudden death after a full meal. It is a purely normal phenomenon, due to the rapid absorption, at certain periods during digestion, of oleaginous substances from the intestine. It can be observed at any time in the dog by feeding him with fat meat, and drawing blood, seven or eight hours afterward, from the carotid artery or the jugular vein.

This condition lasts for a varying time, according to the amount of oleaginous matter in the food. When digestion is terminated, and fat ceases to be absorbed, its transformation continuing to take place in the blood, it gradually disappears from the vascular system; and, finally, when the whole of it has been disposed of by the nutritive process, the serum again becomes transparent, and the blood returns to its ordinary condition.

In this manner the nutritive elements of the food, prepared by the digestive process, are taken into the circulation under the forms of peptone, glucose, and chyle, and accumulate as such at certain times in the blood. But these conditions are temporary and transitional. The absorbed materials soon pass into other forms, and become assimilated to the preëxisting elements of the circulating fluid, thus accomplishing finally the object of digestion, and replenishing the blood with its nutritive elements.

Absorption of Carbohydrates and Production of Glycogen in the Liver.

The absorption of starchy and saccharine matters, and the changes which they undergo while passing through the liver to the general circulation, have been the subject of extended observations, and require a special description. They are connected with the production of glycogen in the liver, as well as with its transformation and disappearance.

If the liver of a carnivorous or herbivorous animal, after twenty-four hours' fasting, be taken from the body immediately after death, finely divided, and boiled for a few moments in water with animal charcoal or an excess of sodium sulphate, to eliminate the albuminous and coloring matters, the filtered fluid will be nearly clear, or will show only a moderately opaline tinge. But if the same thing be done within a few hours after feeding, the watery decoction of the liver will be strongly opalescent; containing in considerable quantity a matter which communicates to the solution a partial turbidity. This matter is *glycogen*, which is present in varying quantity under these two conditions.

Origin and Formation of Glycogen.—As this substance is present in the liver tissue of both carnivorous and herbivorous animals, it may be derived from the materials of either kind of food. In the carnivora, at least, there is evidence that it is supplied from nitrogenous materials, by the nutritive changes which they undergo in the liver. Under some circumstances a material resembling glycogen, or identical with it, may be present in the muscles of the herbivora. Bernard has found it in the muscular tissue in rabbits, and especially in pigeons, when fed on the cereal grains, and in horses kept on oats and barley; but in all these animals it disappears when the food is changed, or after some days' fasting. Luchsinger* has also found it absent from the muscles of the rabbit after several days' fasting, but more persistent in the pectoral muscles of the fowl under similar conditions.

It is accordingly not a constant but only an occasional ingredient of muscular flesh, and when present is usually in very small quantity. Poggiale,† in many experiments instituted for this purpose by a Commission of the French Academy of Sciences, found glycogen in ordinary butcher's meat only once. We have also found it absent from the fresh meat of the bullock's heart, when examined in the manner above described. Nevertheless, in dogs fed exclusively for eight days on this food, glycogen may be abundant in the liver, while it does not exist in other internal organs, as the spleen, lungs, and kidneys.

Glycogen is produced in the liver in especial abundance, after the ingestion of starchy and saccharine food. Bernard ‡ found the decoction of the liver tissue in dogs, after feeding for two days with bread and starch paste, very turbid and milky in appearance. Subsequent experiments by the same observer § have shown that a starchy diet augments notably the quantity of glycogen in the liver. This fact was first demonstrated in a special manner by the observations of Pavy,‖ who, by comparative experiments on dogs fed with animal and vegetable food. found that the influence of the latter was to increase decidedly the weight of the liver, and also the percentage of glycogen which it contained. The same effect was produced by a diet of animal food and sugar. The following table gives the average results of three series of observations by Pavy:

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* Archiv für die gesammte Physiologie. Bonn, 1873, Band viii., p. 290.

† Journal de la Physiologie. Paris, 1858, p. 558.

‡ Leçons de Physiologie Expérimentale. Paris, 1855, p. 159.

§ Revue des Sciences Médicales. Paris, 1874, tome iii., p. 34.

‖ Nature and Treatment of Diabetes. London, 1862.

PRODUCTION OF GLYCOGEN, IN DOGS, UNDER VARYING DIET.

Diet for several days previously.	Weight of liver, in percentage of bodily weight.	Glycogen in the fresh liver, per cent.
Tripe	3.03	7.19
Tripe and sugar	6.42	14.50
Meal, bread, potatoes . . .	6.06	17.23

Experiments on the rabbit also showed that in this animal both the weight of the liver and its percentage in glycogen are much diminished by fasting, but are maintained at the maximum standard, for a time at least, by an exclusive diet of carbohydrates. The average results were as follows:

AVERAGE PRODUCTION OF GLYCOGEN IN RABBITS, WHEN FASTING AND WHEN FED ON CARBOHYDRATES.

Diet for three days previously.	Absolute weight of liver (grammes).	Glycogen in the fresh liver (per cent.).
No food	34.02	1.35
Starch and sugar . . .	73.71	16.15

The quantity of glycogen found in the liver by Pavy is greater than that obtained by subsequent observers under similar circumstances; but the fact of the increase of glycogen under the use of carbohydrates has been confirmed by other experimenters. Dock* found, in experiments on the rabbit, that after from 3 to 5 days' fasting the glycogen in the liver was reduced to a very minute quantity, or more frequently was entirely absent. But if, in this condition, a solution of glucose were introduced into the stomach through a catheter, and the animal killed from 19 to 24 hours afterward, the glycogen in the liver amounted to from 0.650 to 1.243 grammes. After even 7 days' fasting, followed by an injection of glucose into the stomach, so short a time as four hours was sufficient to produce an abundance of glycogen in the liver. The deposit of this substance accordingly takes place so rapidly after the ingestion of this kind of food, that no doubt can remain of its being produced from saccharine or starchy substances.

Tscherinow† showed, by his observations on fowls, both the production of glycogen from animal food, and its more abundant deposit under a vegetable diet. He found, in this species, two days' fasting sufficient to reduce the glycogen to a minimum. After a preliminary fast of this duration, the fowls were fed for two or three days with different kinds of food, and then killed and examined. The average results were as follows:

PRODUCTION OF GLYCOGEN IN FOWLS UNDER DIFFERENT KINDS OF DIET.

Diet previous to the experiment.	Glycogen in the fresh liver, per cent.
Fasting, 2 days	0.57
Lean meat, 2 to 4 days	1.40
Barley, 2 days	5.41
Rice, 2 days	7.21
Fibrine and sugar, 2 to 3 days	10.20

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* Archiv für die gesammte Physiologie. Bonn, 1872, Band v., p. 571.

† Archiv für pathologische Anatomie und Physiologie. Berlin, 1869, Band xlvii., p. 102.

It appears furthermore from the experiments of Weiss and Luchsinger * that a similar increase of glycogen will take place in the liver after the ingestion of *glycerine* ($C_3H_8O_3$), but not under the use of fat or of the alkaline tartrates or lactates.

There is accordingly every reason to believe that carbohydrates, when taken with the food, are transported to the liver by the portal circulation, and fixed in its substance under the form of glycogen. It makes no difference, in this respect, whether they be taken as starch or as sugar; since starchy matters are transformed into glucose by digestion in the intestine. It is under the form of glucose, therefore, that they enter the portal circulation and reach the tissue of the liver. The conversion of this substance into glycogen, as shown in a former chapter (page 61), is essentially a dehydration. It is not possible to say in what manner or by what influence this change takes place; but it is one of the simplest methods of transformation for organic substances, and exactly the reverse of that by which glucose is produced from starch in the intestine.

Transformation of Glycogen into Glucose.—The glycogen thus deposited in the liver from the products of digestion does not remain under that form in the hepatic tissue. It is gradually reconverted into glucose, and carried away into the general circulation. This is shown by the fact that the liver always contains a small quantity of glucose, even in the intervals of digestion, though none may be present in the blood of the portal vein; and that the blood generally contains about the same quantity of glucose, though the supply of carbohydrates in the food be temporarily suspended. The first fact was discovered by Bernard † in 1848. If a dog, cat, or other carnivorous animal be killed after several days of an exclusive meat diet, the liver alone of all the internal organs is found to contain glucose. The hepatic tissue, ground to a pulp and boiled in a little water with an excess of sodium sulphate, to eliminate the albuminous and coloring matters, will yield a filtered extract which responds to Trommer's or Fehling's test, and enters into fermentation on the addition of yeast. At the same time neither the contents of the intestine, the blood of the portal vein, nor any other of the solid organs give evidence of a similar ingredient. By the use of Fehling's test the proportion of saccharine matter in the liver substance may be determined.

The presence of glucose in the liver under these circumstances is common to all animals so far as known. It has been found by Bernard in the monkey, dog, cat, rabbit, horse, ox, sheep, birds, reptiles, and several fish. If the fresh liver of man be examined after sudden death by accident or violence, it is also found to contain sugar.

The glucose thus produced in the liver originates by transformation from the hepatic glycogen under the influence of a ferment. As the

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* Archiv für die gesammte Physiologie, 1873, Band viii., p. 290.

† Comptes Rendus de l'Académie des Sciences. Paris, 1850, tome xxxi., p. 571.

organ usually contains a store of glycogen derived from the last digestive process, the conversion of this substance into glucose will go on after death, and even in the separated liver, at the temperature of 38° C. If the liver of a healthy dog be taken out immediately after death and injected with water by the portal vein, the fluid which escapes by the hepatic vein, after traversing the liver tissue, contains sugar. But as the injection is continued, the quantity of glucose extracted by it from the liver grows constantly less; until in from half an hour to an hour it is completely exhausted, and neither the injected fluid nor the hepatic tissue contains any further trace of glucose. If such a liver be kept in a moderately warm place for some hours its tissue will again become saccharine. Its glucose may be exhausted by a fresh injection, and again reproduced until all the glycogen has been transformed, or until decomposition begins to be established. The glycogen, being less soluble than sugar, remains behind after such an injection and produces a new supply of glucose by a new transformation.

After death, accordingly, if the liver be allowed to remain saturated with its natural juices, this transformation goes on for a time, and the glucose of the hepatic tissue increases at the expense of its glycogen. This fact is established by the experience of all observers. According to our own observations on the dog, the glucose in the liver is increased within an hour after death to four or five times its former quantity. Afterward the change goes on more slowly, its rate diminishing with the lapse of time, so that at the end of twelve hours the sugar may hardly exceed five or six times its original amount. The following table gives the result of three experiments in this direction:

PROPORTION OF GLUCOSE IN THE LIVER OF THE DOG AT DIFFERENT PERIODS AFTER DEATH.

	At the end of	Per thousand parts.
No. 1.	5 seconds	810
	15 minutes	792
	1 hour	10.260
No. 2.	5 seconds	3.850
	6 hours	11.458
No. 3.	4 seconds	2.675
	1 hour	11.888
	4 hours	13.361
	12 hours	15.351

It has been denied by some writers (Pavy, Meissner, Ritter, Schiff) that glucose exists in the liver during life; the whole of it being considered as the product of a change after death. But there is abundant evidence of its existence at the moment of death, or when pieces of the hepatic substance are excised from the living animal; and even its quantity under these circumstances is nearly uniform, varying from about 2 to 4 parts per thousand of the liver tissue. Harley,* who

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* Proceedings of the Royal Society of London, 1860, vol. x., p. 289.

killed the animal by section of the medulla oblongata, immediately placing a portion of the liver in a freezing mixture, and afterward slicing it into boiling acidulated water, has shown that glucose may be demonstrated in the organ within 20 seconds after death. If a portion of the liver, separated while the circulation is going on, be ground to a pulp and plunged into strong alcohol or boiling water, either of which arrests the transformation of glycogen, its decolorized extract will give the reaction of glucose by Fehling's test. We have invariably obtained this result in experiments of this kind,* though the time occupied in taking out the liver tissue and immersing it in alcohol or boiling water was, on the average, but little over six seconds. Bernard,† in a re-examination of the subject after a long interval, found that in dogs and rabbits pieces of the liver, cut out and plunged into boiling water for two or three seconds, constantly contained glucose in nearly the above proportions; and the same conclusion has been reached by Seegen and Kratschmer‡ in experiments on dogs, cats, and rabbits, in which the time varied from a few seconds to three minutes. It appears, therefore, that glucose is a normal ingredient of the liver tissue during life.

Absorption and Disappearance of the Liver-sugar.—The glucose produced in the liver from the transformation of glycogen does not remain at the place of its formation. It is absorbed by the blood traversing the capillaries of the organ, and carried away in the current of the circulation. This is shown by the fact that the blood of the hepatic vein, as well as the liver tissue, contains glucose, although there may be none in the portal blood by which the organ is supplied. As the blood, before its entrance into the liver, in these cases, is destitute of sugar, and yet contains this substance after its passage, it must acquire its saccharine ingredient in the liver itself. Bernard§ has shown that if two specimens, one of portal and one of hepatic blood, be taken from the same dog, when fasting or after an exclusive diet of animal food, the former will show no trace of sugar, while the latter will be saccharine. Lehmann‖ obtained similar results in dogs and horses.

Glucose, accordingly, although constantly produced in the liver, does not accumulate in the organ during life beyond a very moderate quantity. It is only after death, when the circulation has come to an end, and while the transformation of glycogen is still going on, that the proportion of glucose in the liver tissue becomes notably increased. The circulation of blood, so long as it continues, acts like an injection through the hepatic vessels, and extracts from the organ the sugar produced at the expense of its glycogen.

In this way the blood of the general circulation is supplied with

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* Transactions of the New York Academy of Medicine, 1871. 2d Series, Vol I., p. 28.

† Comptes Rendus de l'Académie des Sciences. Paris, 1877, tome lxxxiv., p. 1201.

‡ Archiv für die gesammte Physiologie. Bonn, 1880, Band xxii., p. 214.

§ Leçons de Physiologie Expérimentale. Paris, 1855, pp. 265, 469.

‖ Comptes Rendus de l'Académie des Sciences. Paris, 1855, tome xl., p. 585.

glucose from the liver. According to the more recent investigations of Bernard,* the arterial blood of both herbivorous and carnivorous animals, either fasting or in digestion, and that of man, living on a mixed diet, always contains glucose in sensibly the same proportion; namely, from 1.10 to 1.45 per thousand parts. In its passage through the general capillary circulation, the glucose disappears. The precise changes which it undergoes, and the immediate products of its decomposition, are still unknown, but they no doubt serve in some way for the process of general nutrition. Consequently the venous blood returning from the peripheral organs contains less glucose than the arterial blood with which they are supplied. In two instances Bernard found in the dog its proportion, in the blood of the carotid artery and jugular vein, as follows:

Proportion of Glucose in the Blood.

From the	Per thousand parts.	
Carotid artery	1.14	1.23
Jugular vein	0.98	0.81

In the venous blood of the trunk and lower extremities the same diminution occurs; but at the level of the hepatic veins the quantity of glucose in the blood suddenly augments to more than double, rising sometimes to a maximum of 2.50 or 3.00 parts per thousand. This proportion is again diminished on its being mingled with the blood of the superior vena cava, and in the right ventricle the maximum is 1.81 per thousand parts.

So far, therefore, we must regard the liver as a temporary deposit for the carbohydrates in the form of glycogen. According to this view, the system requires for its nutrition a constant supply of glucose, to be decomposed in the general circulation. The starchy matters of the food, at each period of digestion, are rapidly converted into soluble glucose, and absorbed from the intestine by the portal blood. On reaching the liver they are reduced to the dehydrated or glycogenic condition, under which form they remain as a reserve material until a further supply shall be received from the food. During this interval, the glycogen is slowly reconverted into glucose, and given up, little by little, to the blood of the general circulation, to be decomposed in the system at large. The proportion of glucose in the blood is thus maintained at nearly a constant standard, notwithstanding the variations in its supply from without.

Accumulation of Glucose in the Blood, and its Discharge by the Urine.—Under ordinary conditions the glucose thus formed does not pass beyond the general circulation. But if from any cause its quantity in the blood be raised above a certain proportion, it fails to be completely assimilated, and a part is discharged by the kidneys, producing

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* Comptes Rendus de l'Académie des Sciences. Paris, 1876, tome lxxxii., pp. 369, 407.

a condition of diabetes. Von Becker* found that in rabbits, if glucose be present in the blood in the proportion of 5 parts per thousand, it passes off by the urine, where it may be recognized by the copper test; but if less abundant than this, its indications in the urine are faint and uncertain. Bernard,† by injecting a solution of glucose into the veins of the rabbit, generally produced a condition of diabetes when the glucose was injected in larger quantity than one part per thousand of the bodily weight. The effect of such injections is, however, temporary, passing off when the surplus of saccharine matter has been expelled from the system. According to Von Becker, a solution of glucose, injected into the jugular vein of the rabbit in sufficient quantity, may cause the appearance of sugar in the urine in less than three hours; but at the end of six or seven hours the whole of it may be eliminated, so that it is no longer found in the excretions.

A variety of circumstances may so increase the proportion of glucose in the blood as to cause a saccharine condition of the urine.

I. One of these causes is *an unusually abundant and rapid absorption of sugar from the intestine.* Where a very large quantity of sugar is suddenly absorbed, and at once carried by the portal vein to the liver, this organ is not capable of immediately converting the whole of it into glycogen. A portion thus passes the hepatic circulation unchanged, and, reaching the general circulation in unusual quantity, is discharged with the urine. Von Becker observed that when concentrated solutions of glucose are introduced in abundance into the intestine of the rabbit, it may subsequently appear in the urine. Bernard also found that if in the rabbit, after one or two days' fasting, sugar in large amount be injected into the stomach, the urine becomes diabetic; and he observed the same thing in the human subject, in consequence of taking a large quantity of sugar in solution when the stomach had been empty for several hours. This result is produced only when a much greater abundance of sugar is present in the intestine than in ordinary digestion, and depends on the excessive quantity absorbed in a short time.

II. A diabetic condition may also be induced by anything which *hastens the circulation through the liver*, or increases its supply of blood. Many observers have met with this result from a variety of causes. Bernard found that in dogs the venous blood may present traces of glucose after the abdomen has been subjected to pressure or manipulation over the region of the liver, and after continued struggles or convulsive action, by which the abdominal organs are forcibly compressed. In the same animal, according to Harley, the injection of weak solutions of ammonia or ether into the portal vein may be followed by a saccharine condition of the urine. It has also been observed in man, after a bruise in the right hypochondriac region. The resistance

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* Zeitschrift für wissenschaftliche Zoologie, Band v., p. 176.

† Leçons sur les Liquides de l'Organisme. Paris, 1859, tome ii., p. 73.

of an animal to the inhalation of ether and his subsequent muscular relaxation, general paralysis from fracture of the skull with cerebral hemorrhage, and the action of curare, which also causes complete muscular paralysis, are all known to be sometimes followed by sugar in the urine. Schiff* has even found that, in various animals, compression of the abdominal aorta for ten minutes, or tying the principal blood-vessels of one limb, may induce, for the time being, a condition of diabetes. All these causes probably operate by accelerating the hepatic circulation.

III. Saccharine urine may also be produced by *puncture of the medulla oblongata* in the floor of the fourth ventricle. This fact, first discovered by Bernard,† is best shown in the rabbit by introducing a narrow chisel-shaped instrument, with the cutting edge directly transversely, through the back part of the skull and the cerebellum, so that it shall pierce the posterior part of the medulla in the median line, without passing completely through its substance. Glucose appears in the urine after one or two hours and continues to be present for several days. The immediate effect of this operation, according to Bernard, is to increase the activity of the abdominal circulation. When successfully performed, the operation causes no serious disturbance of the vital functions, and the animal recovers without permanent injury.

In all the above instances, the appearance of sugar in the urine is temporary, depending on occasional disturbance of the circulation. When, in man, this condition becomes permanent, it constitutes the disease known as *Diabetes mellitus*. In this affection, which is generally progressive and fatal, the urine is increased in quantity, of high specific gravity, and continuously charged with glucose, sometimes in great abundance. Fluctuations are observable in its quantity at different periods of digestion and under the use of different articles of food; saccharine and starchy substances causing its increase, and albuminous matters its diminution. But it usually continues to appear in some proportion, whatever regimen be adopted.

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* Journal de l'Anatomie et de la Physiologie. Paris, 1866, No. iv., p. 365.

† Leçons de Physiologie Expérimentale. Paris, 1855, p. 290.

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CHAPTER III.

THE BLOOD.

THE blood is a thick, opaque fluid, varying in different parts of the body from a brilliant scarlet to a dark purple or nearly black color. It has a slightly alkaline reaction, and a specific gravity of 1055. It consists, first, of a nearly colorless, transparent, alkaline fluid, the *plasma*, containing water, albuminous matters, and salts, in solution; and, secondly, of distinct corpuscles, or *blood globules*, swimming in the liquid plasma. The globules form about 40 per cent., the plasma about 60 per cent. by volume, of the entire mass. The specific gravity of the two is somewhat different. That of the plasma is about 1030; that of the globules, 1088. Their relative quantities, by weight, are therefore more nearly equal than when estimated by volume; the exact proportions, according to Robin, being nearly 45 per cent. of globules and 55 per cent. of plasma.

Notwithstanding the difference in specific gravity between the blood-globules and plasma, the natural movement of the blood in the circulation keeps them thoroughly mingled; and even when it is allowed to remain at rest, the globules subside very slowly and imperfectly. Thus the globules, uniformly disseminated through the plasma, give to the blood an opaque aspect and deep red color.

The globules of the blood are of two kinds, red and white; of which the red are far the most numerous.

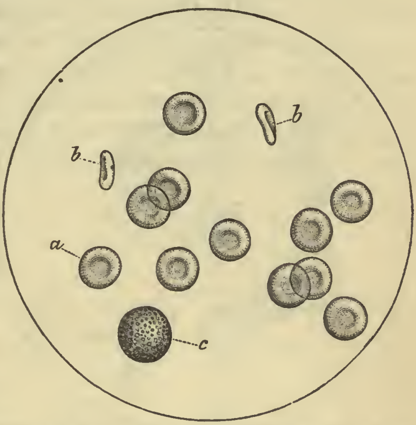
Red Globules of the Blood.

The red globules of human blood are so abundant that, in the thinnest layer under the microscope, they cover or touch each other in every direction. According to the estimates of Welcker and Vierordt about 5 millions are contained in each cubic millimetre of blood. On account of their quantity therefore, as well as their properties, they form a most important constituent of the circulating fluid.

Physical Properties of the Red Globules.—The red globules of human blood present, under the microscope, a circular figure and a smooth exterior. According to the most recent measurements, they have, on the average, a transverse diameter of from 7.50 to 7.75 mmm. Their size varies more or less, but this variation is not very marked for the greater number, and, according to Schmidt, over 90 per cent. of those contained in a single specimen have the same dimensions. The smallest size observed is 4.50 mmm. (Harting), and the largest 9.3 mmm.; while their average diameter, in different individuals, varies from 6.70 to 8.20 mmm.

The form of the red blood-globule is that of a spheroid, much flattened on its opposite surfaces, somewhat like a thick piece of money with rounded edges. If seen flatwise it shows a broad surface and a circular outline (Fig. 43, *a*); but if made to roll over, it presents, during its rotation, the flattened form indicated at *b*. Its thickness is about one-fifth of its transverse diameter. When lying on their broad surfaces, it can be seen that the globules are not exactly flat, but that there is on each side a central depression, the rounded edges being thicker than the middle portion. This produces a different appearance of the globules when examined within and without the exact focus of the microscope. The substance of which they are composed is more refractive than the plasma in which they are immersed. When viewed, therefore, by transmitted light, their thick edges act as double convex lenses, and concentrate the light above the level of the fluid. Consequently, if the object-glass of the microscope be slightly raised, so that the globules fall beyond its focus, their edges will appear brighter. But their central portions act as double concave lenses, and disperse the light from a point below the level of the fluid. They thus become brighter when the object-glass is carried downward and the globules fall within its focus. An alternating appearance of the globules may, therefore, be produced by viewing them first beyond and then within the focus of the instrument. When beyond the focus, they are seen with a bright rim and a dark centre. Within it, they have a dark rim and a bright centre.

Fig. 43.



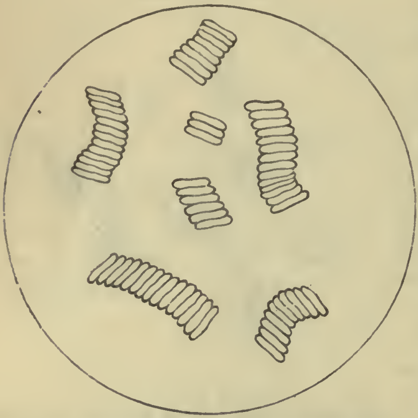
Human Blood-Globules.—*a*. Red globules, seen flatwise. *b*. Red globules, seen edgewise. *c*. White globule.

When placed under the microscope, the blood-globules, after a fluctuating movement of short duration, often arrange themselves in slightly curved rows, adhering to each other by their flat surfaces, and presenting an appearance like that of rolls of coin. This is probably due to the coagulation of the blood, which takes place very rapidly when in thin layers and in contact with glass surfaces; thus forcing the globules into a position to occupy the least space.

The color of the blood-globules, viewed by transmitted light and in thin layers, is a light amber or pale yellow. By reflected light, or in thick layers, it is deep red. Their consistency is nearly fluid. They are very flexible, and easily elongated, bent, or distorted in passing through the narrow channels and currents, often seen in a drop of blood under microscopic examination; but they regain their original shape as soon as the pressure is taken off.

So far as observation can determine, the red globules of the blood, in man and mammalians, are homogeneous in structure; showing no distinction between an external envelope and the parts within. Although some microscopists of high repute (Kölliker, Richardson) continue to regard the existence of an exterior membrane as probable, it is not generally admitted, and cannot be directly demonstrated. Each globule appears like a mass of organic substance of the same color, consistency, and composition throughout.

Fig. 44.



Red Globules of the Blood, adhering together, like rolls of coin.

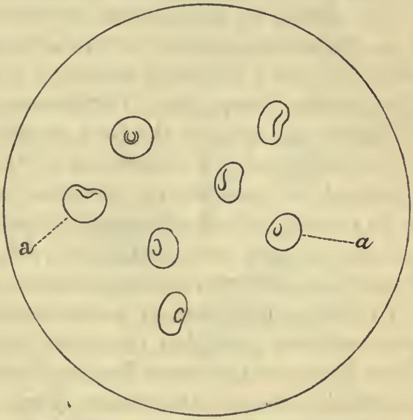
The blood-globules are altered by various physical and chemical agents. If a drop of blood under the microscope be not protected from evaporation, the globules near the edges of the preparation often diminish in size, becoming shrivelled and notched at their margins; an effect apparently due to the partial loss of their watery ingredients. This alteration sometimes takes place with great rapidity in blood withdrawn for examination; but, according to Kölliker, it is never seen in the blood while circulating in the vessels.

Fig. 45.

Red Globules of the Blood, shrunken, with their margins notched.

If water, on the other hand, be added to the blood, the red globules absorb it by imbibition, lose their central concavity, assume the spherical form, and become paler. A large quantity of water may completely extract the coloring matter, leaving the globules as pale, colorless circles, almost invisible from their tenuity. In this condition they may again be brought into view by adding an iodine solution, which stains them of a yellowish color. If water be added in quantity just sufficient to be imbibed by the globules, without extracting their coloring matter, a special change in their form is exhibited. Their thick edges, absorbing water more abundantly than the rest, become turgid, and encroach gradually on the central part. The central depression, under these circumstances, may disappear on one side before it is lost on the other, so that the globule, as it swells up, curls over laterally, and assumes a cup-shaped form. (Fig. 46, *a, a.*) This may often be seen in blood-globules after soaking for some time in the urine, or other animal fluids of less density than the plasma of the blood. Dilute acetic acid at once extracts the coloring matter of the globules, reducing them to the condition of pale and nearly invisible colorless bodies, which, however, remain for a long time, and are dissolved very slowly in comparison with the coloring matter.

Fig. 46.



Red Globules of Blood, after the imbibition of water.

Dilute alkaline solutions, on the contrary, readily dissolve the whole substance of the blood-globules. A solution of potassium hydrate, in the proportion of ten per cent., acts most rapidly in this manner. Solutions of soda and ammonia have a similar effect, though less promptly than the preceding.

Solutions of sodium glycocholate or taurocholate, in any grade of concentration, or of the fresh bile itself, as shown by Kühne, also dissolve the red globules of the blood.

Composition of the Red Globules.—The red globules are composed of an albuminous and a coloring matter, with mineral salts and water. According to Lehmann, the water of the red globules amounts to 688 per thousand parts; a little over 8 parts per thousand consisting of mineral salts, namely, sodium and potassium chlorides, phosphates, and sulphates, together with lime and magnesium phosphates.

The most important ingredient of the red globules is their coloring matter, or *hemoglobine.* According to the estimates of Preyer,* founded on the observed quantity of iron as an ingredient, the average proportion of hemoglobine in human blood is 12.34 per cent. As the globules constitute 45 per cent. of the entire blood, the quantity of hemoglobine in each globule is about 27 per cent. of its mass, or 86 per cent. of its solid ingredients. It is accordingly the principal substance of which the globules are composed.

In the fresh globule the hemoglobine is united with a colorless albu-

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* Die Blutkrystalle. Jena, 1871, p. 117.

minous matter, which forms a substratum for its other ingredients. This substance is less soluble in water than hemoglobine, and remains behind when the latter has been dissolved out, leaving the globules decolorized and reduced in volume. The exact condition of hemoglobine in the blood-globule, and its mode of union with the colorless substratum, are not positively known. Preyer calculates that the water of the globule is insufficient to hold in solution the quantity of hemoglobine present; and on the other hand, as the crystals of hemoglobine are doubly refracting, while the fresh globules are not so, the hemoglobine cannot exist in the globules in a solid form. So far as we can judge, the two substances are uniformly united in a condition of semi-fluidity; but the hemoglobine, being more easily affected by various dissolving agents, may be extracted by this means from the mass of the globule.

The avidity of hemoglobine for free oxygen, and its readiness to part with this substance under favorable conditions, cause it to assume alternately the two different forms of "oxyhemoglobine" and "reduced hemoglobine" (page 94). The former gives its bright scarlet hue to arterial blood, the latter is the dark purple coloring matter of venous blood.

Red Globules of the Blood in Different Classes of Animals.—In all vertebrate animals the red globules contain a coloring matter identical, in its optical and physiological properties, with that of human blood; but they present varieties of form, size, and structure more or less characteristic of different classes, families, and species.

In the *mammalians*, or warm-blooded quadrupeds, the red globules have without exception the same homogeneous structure as in man. They have also the same circular disk-like figure, except in the family of camelidæ (camel, dromedary, lama), where the disks are oval. Their size varies much in extreme cases, the smallest known being those of the Java musk-deer, an animal not larger than a rabbit, which have a diameter of 2.50 mmm., while the largest are those of the elephant, which measure 9.20 mmm. Their size, however, does not always correspond with that of the animal, since those of the cat are larger than those of the sheep, and those of the rabbit larger than either. The following list gives the size of the red globules in various species according to the measurements of Gulliver and Welcker:

DIAMETER OF THE RED BLOOD-GLOBULES OF MAMMALIANS, in Micro-Millimetres.

Elephant	9.20	Fox	6.10
Sloth	8.93	Ox	5.95
Ape	7.35	Horse	5.43
Dog	7.30	Sheep	5.00
Wolf	6.94	Red deer	5.00
Rabbit	6.90	Goat	4.10
Cat	6.50	Musk deer	2.50

In animals where the red globules are small, they are proportionately numerous. It is estimated by Kölliker that the mass of all the red globules together, in any given quantity of blood, does not vary much in different species; but in blood containing the smaller and more abundant globules, their extent of surface, and probably their functional activity, is greater than where they are larger and less numerous. This will also apply to the inferior vertebrate animals, in which the globules are often much larger and less numerous than in man.

In *birds, reptiles, and fish*, comprising all the oviparous vertebrata as well as some which are viviparous, the red globules are distinguished by two marked characters of shape and structure, namely, an oval form and the presence of a nucleus. The only known exceptions are two species of fish, belonging to the family of the Lampreys, in which the globules have a circular outline; but here also they are provided with a nucleus, and are therefore distinguishable from the circular globules of mammalia.

In the Batrachians, or naked reptiles, the red globules present the largest size and exhibit most distinctly their structural character. They are of a regularly oval form, somewhat thicker toward the edges and thinner in the middle, the round or oval, colorless, and granular nucleus projecting slightly from the lateral surface at its central portion. In their reaction under different physical and chemical conditions, they resemble the red globules of mammalians.

In the frog the red globules have a long diameter of 22 mmm., or nearly three times that of the human globules; in Proteus anguinus, the blind water-lizard of the Carniola grottoes, 58 mmm.; in Menobranchus, a species inhabiting the northern lakes of the United States, 62.5 mmm.; and in Amphiuma tridactylum, the great water-lizard of Louisiana, according to Riddell, they are one-third larger than in Proteus, or about 77 mmm. The following list gives the size of different globules of the oval form.

FIG. 47.

BLOOD-GLOBULES OF FROG.—*a*. Red globule seen edgewise. *b*. White globule.

LONG DIAMETER OF THE OVAL RED GLOBULES OF BIRDS, REPTILES, AND FISH, in Micro-Millimetres.

Fowl	12.1	Triton	29.3
Duck	12.9	Proteus	58.0
Pigeon	14.7	Menobranchus	62.5
Lizard	16.4	Amphiuma	77.0
Alligator	19.2	Perch	12.0
Tortoise	20.0	Carp	13.1
Frog	22.0	Sturgeon	13.4

Diagnosis of Blood, and the distinction between Human Blood and that of Animals.—It is often of consequence to recognize blood in various animal fluids in physiological experiments, and it sometimes becomes important in medico-legal investigations. For this purpose, in the fresh fluids, nothing can be more satisfactory than spectroscopic examination; a very small quantity of hemoglobine being sufficient to yield a spectrum with the characteristic absorption bands. This method has the further advantage that it enables us to detect the presence of blood where its globules have been dissolved or their coloring matter reduced to a fluid condition. The washings of a blood stain may show the spectrum of hemoglobine, although they may not contain any red globules perceptible by the microscope. This, however, only shows the presence of the coloring matter of blood, and allows us to distinguish it from other colored fluids; it does not distinguish between the blood of man and that of animals, since the hemoglobine is the same in all.

But by microscopic examination of the red globules, either when fresh or after having been dried and again moistened, we can often distinguish the blood of an inferior animal from that of man. According to Richardson,* a fragment of dried blood, weighing less than $\frac{1}{180}$ of a milligramme, which has been kept for five years, if decolorized with a weak watery solution (0.75 per cent.) of sodium chloride, and afterward tinted with aniline, may exhibit the blood-globules in such a condition that their size can be accurately measured.

If a blood stain, accordingly, which in watery solution gives the spectrum of hemoglobine, be found to contain oval nucleated globules, it must be the blood of a bird, reptile, or fish; and the oval form alone would show that it is not human blood. The question whether a specimen be composed of human blood may consequently be decided *in the negative* by microscopic examination. But if the specimen contain circular globules, without nuclei, it will be impossible to say whether they belong to human blood, or to that of some animal, such as the ape or the dog, whose globules nearly approach the human in size. In most domesticated quadrupeds, the globules are smaller than in human blood; while in both the sloth and the elephant, they are larger. If it were only required to decide whether a specimen of blood belonged to man, or to the elephant or the musk deer, for example, or even to the goat, no doubt the difference in size of the globules would be sufficient to determine the question.

But within nearer limits of resemblance it would be doubtful, because the size of the globules varies to some extent in each kind of blood; and in order to be certain that a particular specimen were human blood, it would be necessary to show that the smallest of its globules were larger than the largest of those belonging to the animal in question, or *vice versa.* The limits of this variation have been tolerably well defined for human blood, but not sufficiently so for many of the lower animals to make an absolute distinction possible.

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* Monthly Microscopical Journal. London, September 1, 1874, p. 140.

In the examination of stains or blood spots, the difficulty is increased by the fact that the drying and subsequent moistening of the globules introduces another element of uncertainty as to their original size.

Physiological Function of the Red Globules.—The red globules of the blood serve mainly as carriers of oxygen. The readiness with which they absorb this substance from the atmosphere, and their changes of color depending upon its supply or withdrawal, indicate that they have a special relation to its introduction and distribution in the body. As a rule, in animals where the red globules are of large size and few in number, the activity of the vital functions is below the average; while in the species where they are smaller and more numerous, the processes of respiration, circulation, nutrition, and movement are increased in rapidity to a similar degree. The strongly marked physical and chemical characters of the red globules correspond with their importance in the functions of vitality.

White Globules of the Blood.

Beside the red globules the blood contains other cellular bodies, differing from the former in several important particulars. These are the *white globules.* As their name implies, they are destitute of coloring matter, but they present, under the microscope, a glistening appearance, and when collected in large quantity may give to the fluid or clot which contains them a whitish hue. They are much less abundant than the red globules, the average proportion in human blood being one white globule to 300 red. They are nearly spherical in form, and, on the average, 11 mmm. in diameter. They are, accordingly, in human blood, distinctly larger than the red globules.' (Fig. 43, *c.*) They consist of a soft, somewhat viscid, finely granular substance, containing one, two, or three ovoid nuclei. They are less yielding and slippery than the red globules, and adhere more readily to surfaces with which they are in contact. When a little watery fluid is added to a drop of blood under examination, the red globules will be hurried away by the currents produced, while the white globules lag behind, and, if the irrigation be continued, may finally be left alone in the field of the microscope. Their transparency is such that, when slowly rolling over with the current, the granules in their interior may often be seen to rotate past each other, with the motion of the globule. The nuclei are sometimes visible in the fresh globule, but may always be brought into view by the addition of water or of dilute acetic acid. These fluids cause a slight swelling of the globule and an increase of its transparency, by which the nuclei become perceptible as sharply defined ovoid or vesicular bodies, near the central part of the mass. By the prolonged action of acetic acid, a portion of the cell substance becomes condensed about the nuclei in various irregular forms, while the remainder appears transparent and homogeneous, with a delicate circular outline. The final effect of both water and acetic acid is to disintegrate the white globules and cause their disappearance. Dilute alkalies dissolve them with great readiness.

Amœboid Movement of the White Globules.—This movement is so called from its resemblance to those of *Amœba*, a minute animal form, of simple organization, living in fresh-water pools and ditches. It is never perceptible while the blood is circulating normally in the blood-vessels, where the white globules always present a rounded and uniformly granular appearance But soon after the blood has been withdrawn, if maintained at or near its normal temperature, the white globules may be seen to alter their shape in a remarkable way. A portion of the rounded outline of the globule first becomes faint and irregular, flattening out and extending itself into one or more transparent, homogeneous-looking prolongations. These prolongations are alternately protruded and retracted, sometimes extending into long filamentous processes, sometimes into shorter expansions with rounded ends. The variations in form thus produced succeed each other with different degrees of rapidity, according to circumstances. In man and the warm-blooded animals, the blood requires to be kept at about the temperature of the living body, in order that these appearances may be exhibited; but in the cold-blooded animals they may be shown at the ordinary temperature of the air.

Fig. 48.

White Globules of Human Blood; altered by dilute acetic acid.

Beside these changes of form, the white globules of the blood may sometimes be seen, by a similar mechanism, to *move* from place to place. In these cases, the globule first sends out the pale prolongations above described. The granules of the remaining portion are then propelled, by a kind of flowing movement, into the prolongations, which thus become granular, and at the same time assume a more rounded form. The remaining portion is subsequently drawn after

Fig. 49.

Changes in Form of a White Blood-Globule of the Newt (*Triton millepunctatus*), occurring in an interval of seven minutes, and within half an hour after its extraction from the living body.

and into the part previously expanded; and by a continuance of this process the whole mass makes a slow progression across the field of the microscope.

These movements are accomplished, like those of the amœba, by local contractions and relaxations of the substance of the globule. In Amœba princeps the movement of progression may take place at the rate of 73 micro-millimetres per minute, and in some gelatinous animalcules it is so active that it may be followed continuously by the eye. But the movement of the white globules of the blood is much more slowly performed, and, like that of the hour-hand of a clock, is to be distinguished only by noting their change of position after a certain time. The white globules of the frog, on the free surface of the mesentery, may move at a rate, as measured by the micrometer, of 13 micro-millimetres per minute; and similar granular corpuscles, in the connective tissue of the mesentery, may progress at the rate of 3.5 micro-millimetres in the same time. Certain cells in the frog's cornea, regarded by some observers as identical with the white globules of the blood, may change their position in the cornea at the rate of 2.5 micro-millimetres per minute.

The amœboid movement is sometimes seen in the interior of the capillary blood-vessels or small veins, when the globules are imprisoned in a stagnant portion of the blood-plasma. But if the circulation be reëstablished, as the globules again move with the blood current, they cease to be distorted, and resume their rounded form.

The physiological properties and functions of the white corpuscles are not so distinct as those of the red globules. Their great inferiority in number shows that they are less important for the immediate continuance of the vital operations; and the same thing may be inferred from their want of strongly marked specific characters. For while the red globules of the blood vary in appearance to a marked degree in different classes, orders, and families, the white globules present nearly the same general features of size, form, and structure throughout the series of vertebrate animals.

Plasma of the Blood.

The plasma is a transparent, colorless, homogeneous liquid, in which the blood-globules are suspended. It consists of water, holding in solution mineral salts and albuminous matters, with various crystallizable substances of organic origin. Its albuminous matters are the most abundant and important of its solid ingredients. Its average composition, according to the most careful estimates, is as follows:

Composition of the Blood-Plasma.

Water	902.00
Albumen	53.00
Paraglobuline	22.00
Fibrinogen	3.00
Fatty matters	2.50

Crystallizable nitrogenous matters		4.00
Other organic ingredients		5.00
Sodium chloride Potassium chloride Sodium carbonate Sodium and potassium sulphates Sodium and potassium phosphates Lime and magnesium phosphates	Mineral salts	8.50
		1000.00

Of these substances, *albumen* no doubt holds the first place in regard to nutrition, as it presents, in a high degree, the character of a nutritious material. It, in all probability, supplies the greater part of the nitrogenous ingredients of the tissues, and provides for their daily nourishment and renovation. In this process it must suffer a variety of transformations, by which it is converted into the different albumenoid matters characteristic of muscular, nervous, glandular, and other structures throughout the body.

The ingredient next in abundance is *paraglobuline*, the average quantity of which is about one-half that of the albumen. It is closely allied to albumen in its chemical relations, and no doubt also in its physiological action; and it is possible that either one of these substances may be an intermediate stage of production or metamorphosis of the other. The principal distinction between them is that paraglobuline may be thrown down by the addition of sodium chloride in excess, or by passing through the diluted blood-serum a stream of carbonic acid, neither of which agents has any effect on albumen. As both substances are coagulable by heat, they are solidified together on raising the blood-serum to a temperature of 72° C.

The *fibrinogen* of the plasma is the substance which produces the solid fibrine of coagulated blood. It is difficult to obtain in the fluid condition, owing to the rapidity with which it coagulates when blood is withdrawn from the circulation. It is usually separated, in the form of coagulated fibrine, by stirring freshly-drawn blood with glass rods or a bundle of twigs, when the fibrine solidifies in thin layers on their surface. It at first contains, entangled with it, some of the red globules with their coloring matter; but these and other foreign substances may be removed by immersing it for a few hours in running water. It is then a mass of nearly white threads and flakes, of semi-solid consistency, and having a considerable degree of elasticity.

Examined in thin layers, it has a fibroid or filamentous texture. Its filaments are colorless and elastic, and not more than 0.5 mmm. in diameter. They lie, for the most part, parallel with each other, and this is probably their arrangement throughout in the undisturbed fibrinous layer; but when torn up for microscopic examination, they are in many spots interlaced with each other in an irregular network. In dilute acetic acid they become swollen, transparent, and fused into a homogeneous mass, but do not dissolve. They are often interspersed with minute granules, which render their outlines more or less obscure.

Once coagulated, fibrine is insoluble in water, and can only be again liquefied by the action of an alkaline or strongly saline solution, by prolonged boiling at a very high temperature, or by digesting with gastric juice or an acidulated solution of pepsine. These agents, however, produce a permanent alteration in its properties, so that it is no longer the same substance as before.

The quantity of fibrine obtainable from the blood varies in different parts of the body. According to most observers,* venous blood in general yields less fibrine than arterial blood. In the liver and the kidneys its disappearance is so complete that little or none is to be obtained from the blood of the renal and hepatic veins. On this account, the blood in the large veins near the heart is more deficient in fibrine than in those at a distance; since the venous blood coming from the general circulation, and containing a moderate quantity, is mingled, on approaching the heart, with that of the renal and hepatic veins, in which it is nearly or entirely absent.

A certain quantity of *peptone* is also found in the plasma, derived from the products of digestion. Its quantity, according to Robin, varies from 1 to 4 parts per thousand. As it is absorbed from the intestine, and neither accumulates in the plasma nor appears in any of the excretions, it is no doubt transformed into some other substance after its entrance into the blood.

The *fatty matters* of the blood are in largest quantity soon after the digestion of food rich in oleaginous substances. At that period, the emulsioned fat finds its way into the blood, and circulates for a time unchanged; communicating to the serum, when very abundant, a turbid or whitish appearance. Afterward it gradually disappears from the circulation, being either deposited in the fatty tissues or transformed into other products of assimilation.

The *mineral salts* of the plasma are principally sodium and potassium chlorides, phosphates, and sulphates, together with lime and magnesium phosphates. Of these the sodium chloride is the most abundant, constituting nearly 40 per cent. of all the saline ingredients. The sodium and potassium phosphates are important for the alkalescence of the blood-plasma, a property which is essential to the functions of nutrition, and even to the immediate continuance of life; since it enables the plasma to absorb carbonic acid in the capillary circulation, and return it to the lungs for elimination. The alkaline carbonates also take part in the production of this alkalescence, and in the herbivorous animals are its principal cause; while in the carnivora the phosphates are more important in this respect. In man, under an ordinary mixed diet, both the phosphates and carbonates are present in varying proportion.

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* Robin, Leçons sur les Humeurs. Paris, 1874, pp. 137, 140, 172.

The *earthy* phosphates of the plasma, which by themselves are insoluble in alkaline or neutral fluids, are held in solution in the blood by union with its albuminous ingredients.

Coagulation of the Blood.

Within a few moments after blood has been withdrawn from the vessels, it presents the remarkable phenomenon of coagulation or clotting. This process commences at nearly the same time throughout the whole mass, which becomes first somewhat diminished in fluidity, so that its surface may be gently depressed with the end of the finger or a glass rod. It then becomes rapidly thicker, and at last solidifies into a uniformly red, opaque, gelatinous mass, which takes the form of the vessel in which the blood was contained. Coagulation usually commences, in man, in from ten to twelve minutes after the blood has been drawn, and is completed in about twenty minutes. In most animals, it is more rapid than this, taking place in the dog, ox, and sheep often within five minutes. In the horse, on the other hand, it is exceptionally slow, requiring a longer time than in man.

The coagulation of the blood is dependent on the presence of its fibrine-producing ingredient. This may be demonstrated in various ways. First, if freshly drawn frog's blood be mixed with a solution of sugar of one-half per cent., and placed on a filter, the blood-globules will be retained; and the transparent colorless filtered fluid after a time coagulates like fresh blood. Secondly, if horse's blood, which coagulates slowly, be drawn from the veins into a cylindrical vessel and allowed to remain at rest, by the time coagulation takes place the blood-globules will have partially subsided, leaving at the surface a layer which is colorless and semi-transparent, but as firmly coagulated as the rest. Thirdly, if horse's blood, freshly drawn into such a vessel, be surrounded by a freezing mixture, and kept at the temperature of 0° C., coagulation is suspended, and the globules sink towards the bottom, leaving a colorless fluid above. If this be removed by decantation, and allowed to rise in temperature a few degrees, it coagulates like fresh blood.

These facts show that the blood-globules take no direct part in coagulation; and that, when present, they are simply entangled in the solidifying clot.

Finally, if the freshly drawn blood of man, or of any warm-blooded animal, be stirred with a bundle of twigs or glass rods, the fibrine coagulates in comparatively small mass on the surface of the foreign bodies; and the globules entangled in it may be washed out without changing its essential character.

It is the fibrinogen, therefore, which, by its coagulation, induces the solidification of the entire blood. As it is uniformly distributed throughout, when coagulation takes place its filaments entangle in their meshes the globules and albuminous fluids of the plasma. A very small quantity of fibrine is sufficient to include in its solidification all the fluid and semi-fluid ingredients of the blood, and to convert the whole into a jelly-like, coagulated mass.

As soon as the coagulum is formed, it begins to contract, increasing in consistency as it diminishes in size. By this means the albuminous liquids are pressed out from the meshes in which they were entangled. They first exude upon the surface as isolated drops, which soon increase in size and number. After a time they coalesce in all directions, until the whole surface is covered with fluid. The clot at first adheres closely to the sides of the vessel; but as contraction goes on, it separates, and fluid exudes between it and the vessel. This continues for ten or twelve hours; the clot growing constantly smaller and firmer, and the expressed fluid more abundant.

The globules, owing to their greater consistency, do not escape with the albuminous fluids, but remain entangled in the coagulum. At the end of twelve hours the blood is completely separated into two parts, namely, the *clot*, a red, opaque, semi-solid mass, consisting of fibrine and blood-globules; and the *serum*, a transparent, nearly colorless fluid, containing the watery, albuminous, and saline matters of the plasma.

The change of the blood in coagulation may be expressed as follows:

Before coagulation it consists of

1st. Globules; and 2d. Plasma—containing
- Fibrinogen,
- Albumen,
- Paraglobuline,
- Water,
- Salts.

After coagulation it is separated into

1st. Clot, containing
- Fibrine and
- Globules;

and 2d. Serum, containing
- Albumen,
- Paraglobuline,
- Water,
- Salts.

Conditions favoring or retarding Coagulation.—The coagulation of blood is influenced by various physical conditions. In the first place, it is suspended by a freezing temperature. If blood be drawn into a narrow vessel surrounded by a freezing mixture, and rapidly cooled down to 0° C., coagulation does not occur, and the blood remains fluid so long as the temperature is at this point.

Secondly, coagulation is prevented by the presence of certain neutral salts in large quantity. If fresh blood be allowed to mingle with a concentrated solution of sodium sulphate, no coagulation takes place. This is not because the coagulable material has been destroyed; since, if the mixture be diluted with six or seven times its volume of water, so as to reduce its concentration, the fibrine solidifies in a few moments as usual.

Coagulation of the blood may be hastened or retarded by variations in the manner of its withdrawal from the veins, or in the surfaces with which it comes in contact. If drawn rapidly from a large orifice, it remains fluid for a comparatively long time; if slowly, from a narrow orifice, it coagulates quickly. The shape and structure of the vessel into which it is received also exert an influence. The greater the surface over which the blood comes in contact with the vessel, the more is coagulation hastened. If allowed to flow into a tall, narrow, cylindrical vessel, or a shallow plate, it coagulates more rapidly than if received in a hemispherical bowl, in which the extent of surface is less, in proportion to its capacity. For the same reason, coagulation takes place sooner in a vessel with roughened surface than in one which is smooth; and blood coagulates most rapidly when spread out in thin layers, or entangled in cloths or sponges. Hemorrhage, accordingly, continues longer from an incised than from a lacerated wound; because the blood, in flowing over the ragged edges of lacerated tissues, solidifies upon them, and blocks up the orifice.

In all cases there is an inverse relation between the rapidity of coagulation and the firmness of the clot. When coagulation takes place slowly, the clot becomes small and dense, and the serum is abundant. When rapid, it is followed by imperfect contraction of the coagulum, and incomplete separation of the serum, and the clot remains large, soft, and gelatinous.

The blood coagulates in the interior of the vessels *after stoppage of the circulation.* Under these circumstances coagulation takes place less rapidly than in blood withdrawn from the body. In man, as a rule, the blood is found coagulated in the heart and large vessels from twelve to twenty-four hours after death. In most animals, coagulation occurs earlier than this, usually from four to ten hours after death.

Coagulation of the blood takes place also within the body, during life, from *local arrest or impediment of the circulation.* Blood extravasated into the connective tissue, the substance of an internal organ, or a serous cavity, coagulates after a short time, and forms a clot which takes the shape of the cavity occupied. A ligature, placed upon an artery in the living subject, produces coagulation above the ligatured spot. The clot extends from the ligature backward to the next collateral branch, that is, to the point at which the circulation still continues. In an aneurism the blood in the dilated portion of the artery coagulates on the inner surface of the sac. In these cases, as well within as outside the body, and during life as well as after death, stoppage or retardation of the circulatory movement induces, after a time, the coagulation of the blood.

It is asserted, however, that simple stoppage of the local circulation during life will not induce coagulation, unless the inner membrane of the blood-vessel be wounded or irritated. According to Burdon Sanderson, if blood be imprisoned in the jugular vein of the rabbit by carefully compressing the vessel at two points between transverse needles, so arranged as not to wound or bruise the vascular coats, it will remain fluid in this situation for two days; while if ordinary ligatures be applied, a coagulum is formed in the isolated portion of the vein.

From this it would appear that some injury or alteration of the vascular walls is an element in the exciting cause of coagulation. It is of course impossible to withdraw blood from the system without inflicting such an injury; and we know that in cases of phlebitis, coagulation often takes place within the affected veins, when the only condition present to explain it is the inflammatory alteration of the vascular walls.

The coagulation of fibrine is not a commencement of organization. It is simply the passage of one of the ingredients of the blood from its normal condition to a state of solidity. The coagulable matter, when solidified, has lost its natural properties as a constituent of the plasma, and they cannot afterward be restored. The clot, therefore, once formed, even within the body, as in cases of ligature, apoplexy, or extravasation, becomes a foreign substance, and is absorbed by the neighboring parts during convalescence. At first it is comparatively voluminous, soft, and red. Its more fluid parts are then taken up, and it becomes smaller and denser. As absorption goes on, its coloring matter diminishes, and finally disappears. The time required for complete reabsorption of a clot varies, according to its size and situation, from a few days to several months.

Nature of Coagulation.—The coagulation of blood has been the subject of much laborious investigation. The difficulty of understanding its nature depends on the fact that the blood, which continues fluid under normal conditions while circulating in the vessels, solidifies promptly and inevitably on its withdrawal. It is evident that the solid fibrine which we obtain after coagulation is not the material which was present beforehand in the blood; but that it has been produced, by some alteration, from a preëxisting fluid substance. Any theory of the process, to be satisfactory, must explain not only the coagulable property of the fibrine-producing ingredient, but also the fluidity of the blood in its natural condition, notwithstanding that it contains a material so ready to assume the solid form. It is unnecessary to consider the former theories of coagulation, which have now been abandoned as inconsistent with known facts. It is not due to the cooling of the blood, to the contact of air, nor to the escape of a gaseous solvent; since it will occur in the absence of all these conditions. Of late years, the only views on this subject which have attracted general attention are those of Denis, in which coagulation is explained by the decomposition of a previously existing substance, and those of Schmidt, which attribute it to the union of two substances previously distinct.

According to Denis, the blood contains an albuminous matter, termed "plasmine," in the proportion of 25 parts per thousand. When withdrawn from the circulation, it separates into two new substances; namely, fibrine (3 parts per thousand) which coagulates, and paraglobuline (22 parts per thousand) which remains fluid. The basis for this theory is that if fresh blood be drawn into a concentrated solution of sodium sulphate, to prevent its coagulation, and sodium chloride be added to the mixture in the proportion of ten per cent., it throws down a white, pasty substance, which represents 25 parts per thousand of the original plasma. This substance is the so-called "plasmine;" and if redissolved by the addition of water, its solution coagulates, yielding 3 parts of a solid matter, like fibrine, and 22 parts of a liquid substance, having the properties of paraglobuline. The albumen of the plasma (53 parts per thousand) remains in the sodium sulphate solution, not having been precipitated by the addition of sodium chloride.

This theory is defective, because the material termed "plasmine," may be, from the first, a mixture of two different substances, one coagulable and the other not so, but both precipitable from the sodium sulphate solution by sodium chloride. In that case, it would not facilitate the explanation of the process. In point of fact we know that both the fibrine-producing substance and paraglobuline may be thrown down from their solutions by the addition of sodium chloride in excess.

According to the theory of Schmidt, the coagulable fibrine is produced by the union of two previously existing substances, neither being coagulable by itself. One of these substances is fibrinogen, present in the blood in small quantity; the other is paraglobuline, present in large quantity. When the fibrinogen, therefore, has all been converted into coagulated fibrine, there still remains in the serum a surplus of paraglobuline, which may cause coagulation in other liquids, provided they contain fibrinogen. The liquid usually employed to demonstrate this property is that of hydrocele, which does not coagulate spontaneously, but may sometimes be made to do so by the addition of blood-serum.

It was found, however, that both fibrinogen and paraglobuline might be present in a liquid, and yet fail to produce coagulation. The author* of the theory therefore recognized the existence of a third substance, the "fibrine ferment," which was essential to induce the combination of the other two. According to this view, fibrinogen and paraglobuline both exist in the blood while circulating in the vessels; and, when they unite, supply the material for the coagulated fibrine. But the ferment which excites their combination only appears in the blood during or after its withdrawal. It may then be extracted by the process already described (p. 87).

There is no doubt in regard to the existence and character of the fibrine-ferment. Its mode of operation is analogous to that of other organic ferments. In the first place it acts in very small quantity in proportion to the amount of coagulation produced. Secondly, its action is confined within certain limits of temperature, being retarded by cold, and permanently arrested by the heat of boiling water. Thirdly, though precipitable by alcohol, it is not destroyed by this substance, but after precipitation may be redissolved in water, with its properties unchanged. Fourthly, after inducing coagulation, it still remains in the fluid separated by filtration, and may be again repeatedly used for the same purpose, with only a very slow diminution of its activity. This shows that it does not contribute by its substance to the coagu-

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* Archiv für die gesammte Physiologie. Bonn, 1872, Band vi., p. 413.

lated fibrine, being efficient rather by its presence, after the manner of the ferments.

But there is reason to believe that the fibrine-ferment, in inducing coagulation, acts only on the fibrinogen, and that paraglobuline takes no part in the process. According to Fredericq* the quantity of fibrine obtainable from a solution of fibrinogen of known strength, is never greater than that of the fibrinogen itself, coagulated by heat. This would indicate that the fibrinogen alone supplies the material of the coagulated fibrine, by a molecular change in its own substance, like the caseine of milk when coagulated by rennet. Hammarsten† has furthermore satisfied himself that when solutions of paraglobuline induce coagulation in liquids containing fibrinogen, they owe this property to small quantities of ferment with which they are contaminated; and by using special precautions in their purification, he has found that solutions of fibrinogen will coagulate completely on the addition of the ferment, when neither liquid contains any trace of paraglobuline, hemoglobine, or serum-albumen.

The coagulation of fibrinogen is, therefore, without doubt due to the action of a ferment. The fibrinogen, as it exists in the circulating blood, is not coagulable; and it becomes so only by contact with the substance which produces its alteration. The only remaining question is in regard to the source of this ferment, when blood is withdrawn from the vessels or coagulates in their interior. The evidence appears to show that it comes from the divided or injured vascular coats, or from the interstitial spaces beyond. The minute quantity necessary to effect coagulation may be exuded from a wounded surface, however small; and after death it may slowly transude through the membranes, like the coloring matters and serous fluids of the body. But the place and mode of its production can hardly be determined with certainty, until its composition and physical properties are fully known.

Usefulness of Coagulation.—Although the coagulating material of the blood, owing to its small quantity, does not seem to take a large share in nutrition, it is still an important ingredient of the circulating fluid. It is this substance which effects the arrest of hemorrhage from divided or ruptured blood-vessels. Whenever a wound is made in vascular tissues, the blood at first flows freely from the external orifice. But a portion soon coagulates on the edges of the wound, and after a time its successive deposits obstruct the orifice, and prevent further hemorrhage. For wounds of moderate size, in which only veins and capillaries, or small arteries, have been divided, it is sufficient to compress the wound and to keep its edges in contact for fifteen or twenty minutes. By this time the thin layer of blood between the wounded surfaces has coagulated, and when compression is removed hemorrhage does not reappear. If a large artery be opened, the force with which the blood is expelled prevents local coagulation, or may detach the

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* Hoppe-Seyler, Physiologische Chemie. Berlin, 1879, p. 416.

† Archiv für die gesammte Physiologie. Bonn, 1879, Band xix., pp. 563, 581.

coagula after they are formed. In such cases the surgeon places a ligature upon the wounded artery, and in this way controls the hemorrhage. But the ligature is only a means of applying compression for a longer time, and is still temporary, as it must finally come away by ulceration through the coats of the vessel. The essential obstacle to the flow of blood in a ligatured artery is the coagulum formed in the vessel behind the ligature; which, when the ligature is detached by ulceration, has become sufficiently dense and adherent to resist the impulse of the blood.

The importance of coagulation in this respect is shown by the difficulties which follow where it is deficient. In some cases of the ligature of large arteries, in patients exhausted by injury or loss of blood, when the ligature comes away the bleeding begins again, no internal clot having been formed; and a second ligature, applied above the situation of the former one, is again followed by secondary hemorrhage. In certain persons there appears to be a congenital deficiency of the coagulating ingredient of the blood, a peculiarity sometimes observed in several members of the same family; and in these cases, any slight wound, or trivial surgical operation, may be followed by long-continued or fatal hemorrhage.

Entire Quantity of Blood in the Body.—The estimation of the quantity of blood in the living body is surrounded with difficulties. The earliest and simplest method adopted was by suddenly dividing all the vessels of the neck in a living animal and collecting the blood which escaped. But this method is faulty, since the flow of blood ceases, in such an experiment, not because the whole of it has been discharged, but because coagula have formed about the divided vessels, and because the heart's action begins to fail before the vascular system is empty. A certain quantity of blood always remains in the body after death by hemorrhage; amounting sometimes to over 25 per cent. of the entire mass. The animal therefore dies before he has lost quite three-fourths of the circulating fluid.

Of the other methods which have been adopted there are none absolutely free from possible sources of error. The best are those by which, after all the blood is discharged which escapes spontaneously from divided vessels, the circulatory system is injected with a weak saline solution, until the fluid, after traversing the vascular channels, returns colorless. The quantity of blood thus washed out is then ascertained by comparing the fluid of injection with a watery dilution of blood of known strength.

The most accurate process is that employed by Steinberg,* who, after bleeding the animal to death, injected the aorta with a watery solution of sodium chloride, of one-half per cent., until the fluid of injection returned colorless. The whole of it being then mingled, the hemoglobine which it contained was determined as follows by the spectroscopic test: Equal quantities of pure blood, in two similar test-tubes, were diluted.

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* Archiv für die gesammte Physiologie. Bonn, 1873, Band vii., p. 101.

one of them with pure water, the other with the fluid of injection, until each, placed before the slit of the spectroscope, just allowed the green light of the spectrum to be visible. From the relative quantities of the two liquids needed to produce this result, the amount of hemoglobine, and consequently of blood, extracted by the injection could be calculated. This quantity, added to that which had escaped spontaneously from the vessels, gave the entire amount of blood, as follows:

Quantity of Blood, as Compared with the Bodily Weight.

In Dogs,	from	8.00	to	8.93	per cent.
" Cats,	"	8.40	"	9.61	"
" Guinea-pigs,	"	8.13	"	8.33	"
" Rabbits,	"	7.50	"	8.13	"

There is evidence that the quantity of blood varies in the same animal, according to various bodily conditions, and especially the digestive process. Steinberg found that in the cat, while fasting, the percentage of blood was reduced from 8.40 to 5.61 per cent. Bernard* observed that if two animals of the same weight, one in full digestion and the other fasting, be suddenly decapitated, the quantity of blood discharged from the former is greater than that from the latter. He has also shown that, in a rabbit during digestion, twice as much blood can be withdrawn without causing death, as in one of the same weight in the fasting condition. The volume of blood in the body fluctuates, therefore, within certain limits, with the introduction of nutritious matter by digestion and its expenditure during the interval.

The most satisfactory determination of the quantity of blood in man is that by Weber and Lehmann.† These observers operated on two criminals executed by decapitation; the methods and results being essentially the same in both. In one case, the body weighed before decapitation 60.14 kilogrammes; and the blood which escaped spontaneously amounted to 5540 grammes. To estimate the quantity remaining in the vessels, the experimenters injected the arteries of the head and trunk with water until it returned from the veins of a pale red or yellow color, collected the fluid thus returned, and ascertained the amount of its solid matter. The result was as follows:

Blood which escaped from the vessels . .	5540	grammes.
" remained in the body . .	1980	"
Entire quantity, . .	7520	"

The blood, accordingly, amounted during life to 12.54 per cent. of the bodily weight. Bischoff, in a similar observation, in 1855, found it only about 8 per cent. As in Steinberg's experiments the quantity of blood in the cat also varied by 50 per cent. above the minimum, it will probably be near the truth to estimate its average quantity in the human subject at about 10 per cent. of the bodily weight; and a man weighing 65 kilogrammes (143 pounds avoirdupois) would therefore have 6500 grammes, or a little over 14 pounds of blood.

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* Leçons sur les Liquides de l'Organisme. Paris, 1859, tome i., p. 419.

† Physiological Chemistry, Cavendish edition. London, 1853, vol. ii., p. 269.

CHAPTER IV.

RESPIRATION.

THE most constant phenomenon presented by living organisms, both animal and vegetable, is the absorption of oxygen. This substance, either in the gaseous form as a constituent of the atmosphere, or dissolved in water or other liquids, is indispensably requisite for the manifestation of vital phenomena. Oxygen is diffused everywhere over the surface of the earth, forming rather more than one-fifth part of the volume of the atmosphere, and exists in solution in greater or less abundance in the water of springs, rivers, lakes, and seas. Animals and plants, accordingly, whether living in the air or in the water, are surrounded by media in which this substance is present. Even parasitic organisms, inhabiting other living bodies, and the fœtus during intra-uterine life, though not immediately in contact with oxygen, are supplied with nutritious fluids which have themselves been exposed to its influence. *Respiration* consists in the process by which oxygen penetrates the substance of living organisms, and the changes which accompany or follow its introduction.

Respiration in Vegetables.—In regard to vegetables, a distinction is to be made between respiration and the absorption of gaseous matter for the production of organic material. All green plants, under the influence of solar light, absorb carbonic acid and water; partially deoxidizing these substances, to form, with their remaining elements, starch, cellulose, and fat. The oxygen thus separated is exhaled in a free form; while an accumulation of organic material takes place in the vegetable fabric, which thus increases in substance, and may afterward serve for the nutrition of animals. This process, therefore, is not one of respiration, but of organic production. It is peculiar to vegetables, since animals have no power to produce organic material, and depend upon vegetables for their supply of food.

Animals, on the other hand, consume the organic material thus produced, at the same time absorbing oxygen and exhaling carbonic acid and water. In this respect animal and vegetable life stand in a complementary relation to each other. Vegetables produce organic matter by deoxidation; animals consume it with the phenomena of oxidation.

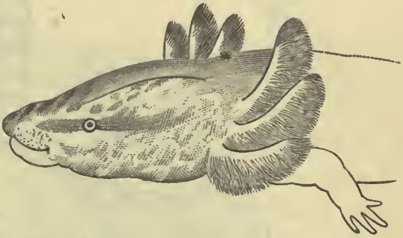
But this apparent opposition only exists because plants have the special power of producing organic matter, by which they become a source of nourishment for animals. The organic substances so produced do not immediately take part in the active phenomena even of vegetable life. They are, on the contrary, deposited in a quiescent form as reserve material, to be afterward transformed and assimilated by the plant, or consumed by animals. In vegetables, as well as in animals, a true respiration also takes place, marked in both instances by the absorption of oxygen. The deoxidizing process, by which organic matter is produced, occurs only in green vegetables, under the influence of solar light; but the absorption of oxygen is a constant phenomenon, taking place in both green and colorless plants, in darkness as well as in the light.

The active phenomena of vegetation, moreover, are dependent on the absorption of oxygen, and cannot go on without it. When the starch stored up in a seed becomes liquefied and converted into sugar, and germination begins, the absorption of oxygen is necessary to its continuance. This is the case not only in germinating seeds, but also in expanding leaf and flower buds, all of which consume in a short period several times their volume of oxygen. The processes of germination, growth, and flowering, as well as the intra-cellular movement of the vegetable plasma, the motions of the sensitive-plant in response to stimulus, and certain periodical movements of the leaves in other species, all cease in an atmosphere deprived of oxygen.* The function of respiration is accordingly essential to every form of vital activity.

Organs of Respiration.

Respiration is very active in the mammalians and birds, less so in reptiles and fishes; and in different classes the organs by which it is accomplished vary in size and structure according to the activity of the function. Its requisite conditions are that the circulating fluid be exposed in some way to the influence of the atmosphere or of an aerated fluid. The respiratory apparatus consists essentially of a moist and permeable respiratory membrane, with blood-vessels on one side and air or an aerated fluid on the other. The blood and the air, consequently, do not come in direct contact with each other, but absorption and exhalation take place through the intervening membrane.

Fig. 50.



HEAD AND GILLS OF MENOBRANCHUS.

In most aquatic animals, the respiratory organs have the form of *gills;* that is, vascular prolongations of the integument or mucous membrane, which are bathed in the surrounding water. In *Menobranchus* (Fig. 50) the gills are external feathery tufts on the sides of the neck, connected, through lateral fissures, with the mucous membrane of the pharynx. Each filament consists of a fold of mucous

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* Mayer, Lehrbuch der Agrikultur-Chemie. Heidelberg, 1871, Band i., pp. 91, 95. Hoppe-Seyler, Physiologische Chemie. Berlin, 1877, p. 171.

membrane, containing a network of capillary blood-vessels. The apparatus is supplied with a cartilaginous framework and a set of muscles, by which the gills are kept in motion, and thus brought in contact with fresh portions of the aerated fluid.

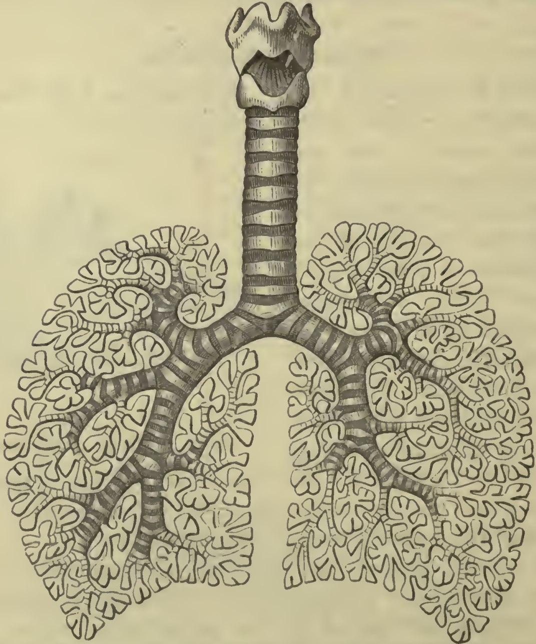
Fig. 51.

Lung of Frog, cut open, showing its internal surface.

In terrestrial and air-breathing animals, the respiratory apparatus is situated internally, under the form of *lungs*. In salamanders and newts, the lungs are cylindrical sacs, communicating anteriorly with the pharynx, and terminating by rounded extremities at the posterior part of the abdomen. The air, forced into them from the pharynx, is after a time regurgitated, to make room for a fresh supply.

In frogs, turtles, and serpents, the lung is divided by incomplete partitions into smaller cavities or "cells." The cells all communicate with the central pulmonary cavity; and the partitions between them are vascular folds of the lining membrane. (Fig. 51.) By this arrangement a greater extent of pulmonary surface is presented to the air, and the aeration of the blood takes place with a corresponding rapidity.

Fig. 52.

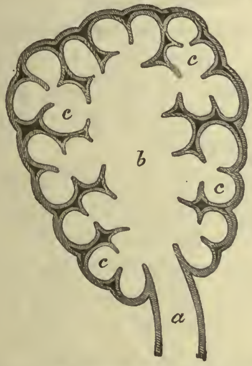


Human Larynx, Trachea, Bronchi and Lungs; showing the ramifications of the bronchi, and division of the lungs into lobules.

In the warm-blooded animals, the lungs are constructed on a plan essentially similar to the above, differing from it only in the greater extent to which the pulmonary cavity is subdivided. In man (Fig. 52) the respiratory apparatus begins with the larynx, communicating, through the glottis, with the pharynx. Then follows the trachea, a membranous tube with cartilaginous rings, dividing into the right and left bronchi. These divide in turn into secondary and tertiary bronchi; the subdivision continuing, and the bronchial tubes growing constantly smaller and more numerous. As they diminish in size, the tubes grow more delicate in structure, and the cartilaginous rings and plates disappear from their walls. When finally reduced to a diameter of 0.3 millimetre, they are composed only of a thin membrane, lined with pavement epithelium, resting upon an elastic fibrous layer. They are then known as the "ultimate bronchial tubes."

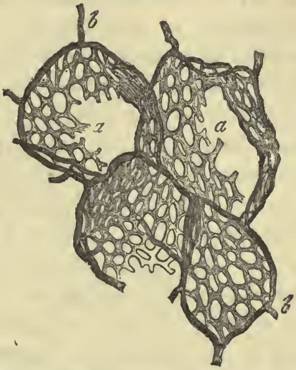
Each ultimate bronchial tube terminates in a pyramidal-shaped islet of pulmonary tissue, about 2 millimetres in diameter, termed a "pulmonary lobule." Each lobule may be considered as representing the frog's lung in miniature. It consists of a vascular membrane in the form of a sac, the cavity of which is divided into secondary compartments by thin partitions projecting from its inner surface. These secondary cavities are the "pulmonary vesicles." They have, according to Kölliker, an average diameter of about 0.25 millimetre; but owing to the distensibility and elasticity of their walls, they are capable of dilating to double or triple their former size, and returning to their original dimensions when the distending force is removed. There is reason to believe that during life they alternately expand and retract, as the lungs are filled and emptied with the movements of respiration.

FIG. 53.



SINGLE LOBULE OF HUMAN LUNG.—*a.* Ultimate bronchial tube. *b.* Cavity of lobule. *c, c, c.* Pulmonary vesicles.

FIG. 54.



NETWORK OF CAPILLARY BLOOD-VESSELS in the Pulmonary Vesicles of the Horse.—*a.* Cavity of Vesicle, with capillary plexus. *b.* Pulmonary blood-vessels, supplying capillary plexus. (Frey.)

Each vesicle is surrounded by capillary blood-vessels, which penetrate its partition walls and are thus exposed on both sides to the influence of the air in the pulmonary cavities. The abundant elastic tissue, in the walls of the vesicles, and in the interlobular spaces, gives to the lungs their property of resiliency. The pavement epithelium lining the ultimate bronchial tubes extends into the lobules and vesicles, forming, according to Kölliker, a continuous investment of their internal surface.

The extensive involution of the respiratory membrane, resulting from the multiplication of the bronchial tubes and vesicles, in the lungs of man and mammalians, increases in a high degree the activity of respiration; since the blood in the capillary vessels, distributed in thin layers over so large a surface, in immediate proximity to the air in the pulmonary cavities, is placed under the most favorable conditions for rapid arterialization.

Movements of Respiration.

The air in the pulmonary lobules and vesicles, being used for the arterialization of the blood, is rapidly altered in composition, and requires to be replaced by a fresh supply. Its renewal is effected by alternate movements of expansion and collapse of the chest, following each other in regular succession, known respectively as the "movement of inspiration," and the "movement of expiration."

Movement of Inspiration.—The expansion of the chest is produced by two sets of muscles, namely, the diaphragm and the intercostals. The diaphragm is a vaulted muscular sheet, forming the floor of the thorax, its edges being attached to the lower extremity of the sternum, the inferior costal cartilages, the borders of the lower ribs, and the bodies of the lumbar vertebræ, whence its fibres run upward and inward, to the triangular tendinous expansion at its centre. In the relaxed condition, its convexity rises into the chest, as high as the level of the fifth rib. When its muscular fibres contract, they draw its central tendon downward, depressing the abdominal organs, and enlarging the cavity of the chest in a vertical direction. At the same time, by the contraction of the intercostal muscles, the ribs are drawn upward and outward, rotating upon their articulations with the spinal column, and expanding the chest from side to side. The sternum also rises slightly and increases to some extent the antero-posterior diameter of the thorax. By these changes, the cavity of the lungs is enlarged in every direction, and the air penetrates, by the force of aspiration, through the trachea and bronchial tubes, to the pulmonary lobules and vesicles.

The action of the respiratory muscles is indicated externally by two different motions, namely, the expansion of the chest, due to the intercostals, and the protrusion of the abdomen, caused by the descent of the diaphragm. In children, as well as in the adult male, under ordinary conditions, the diaphragm performs most of the work, and the movements of the abdomen are the only ones especially noticeable. Any unusual exertion, however, produces an increased expansion of the chest; and the movement of the ribs becomes more plainly visible after walking or running. In the female, the movements of the chest, particularly of its upper half, are habitually more prominent than those of the abdomen; and this difference in the mechanism of respiration is characteristic of the sexes.

In certain abnormal conditions the activity of either the intercostal muscles or the diaphragm may be separately suspended, leaving the work of respiration to be performed by the remaining set of muscles. If the intercostals be paralyzed by injury of the spinal cord in the lower cervical or upper dorsal region, the thorax remains quiescent, while the protrusion of the abdomen is increased to a corresponding degree. This mode of breathing is called *abdominal respiration.*

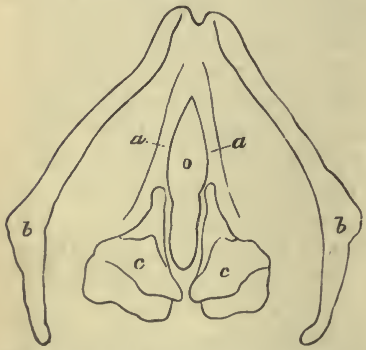
In cases of peritonitis, on the other hand, the movements of the diaphragm are restrained, owing to the tenderness of the inflamed surface. This is known as *thoracic respiration;* since the expansion of the chest becomes more active than usual, and is the only visible movement performed.

Movement of Expiration.—After inspiration is accomplished and the lungs are filled with air, the diaphragm and intercostal muscles relax, and a passive movement of expiration takes place, by which the pulmonary cavity is partially emptied. It is mainly accomplished by the elastic reaction of the lung tissue, which compresses the pulmonary lobules and vesicles, and expels a portion of the contained air. This elasticity is readily shown by removing the lungs from a recently killed animal, distending them by insufflation through the trachea, and then allowing them to collapse. They react, under these circumstances, with sufficient power to expel the larger portion of the injected air. Other organs, during life, aid in the process. The elastic costal cartilages, slightly twisted in inspiration by the elevation of the ribs, resume their original form in expiration, and, by drawing the ribs downward, compress the thorax. Lastly, the abdominal organs, displaced by the descent of the diaphragm, are forced backward by the elasticity of the abdominal walls and of their own fibrous attachments, carrying the relaxed diaphragm before them. By the recurrence of these two movements, of inspiration and expiration, fresh portions of air are alternately introduced into and expelled from the pulmonary cavity.

All the air in the lungs, however, is not changed at each movement. A considerable quantity remains behind after the most complete expiration; and even when the lungs have been removed from the chest, they still contain a certain volume of air, which cannot be displaced by any violence short of disintegrating the pulmonary tissue. Only a comparatively small portion of the air, therefore, passes in and out with each respiratory movement; and its complete renewal will require several successive respirations. The relation in quantity between the air changed at each respiration and that contained in the chest varies with different conditions; but the average results obtained by different observers show that, in general, the volume of the inspired and expired air is from 10 to 13 per cent. of the whole contents of the pulmonary cavity. Thus it will need from eight to ten respirations entirely to renovate the air in the lungs.

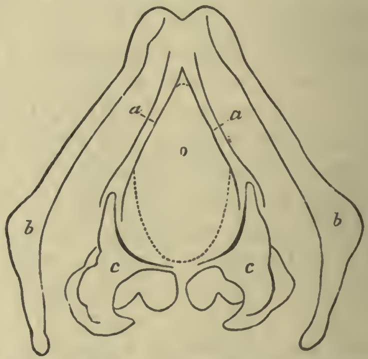
Respiratory Movements of the Glottis.—Beside the movements of respiration belonging to the chest, there are similar changes of expansion and collapse in the larynx. If the respiratory passages be examined after death, the opening of the glottis will be found smaller in calibre than the cavity of the trachea. The air-passage at the level of the glottis is a narrow chink; but it widens considerably in the lower part of the larynx, while the trachea is a spacious cylindrical tube. In man the space between the vocal chords has an area, on the average, of only one square centimetre; while the calibre of the trachea in the middle of its length is 2.81 square centimetres. But this disproportion does not exist during life. In respiration there is a regular movement of the vocal chords, synchronous with that of the chest, by which the size of the glottis is alternately enlarged and diminished. At inspiration the glottis opens, admitting the air freely into the trachea; at expiration it collapses, as the air is expelled from below. These movements are the "respiratory movements of the glottis." They correspond in every respect with those of the chest, and are excited or retarded by similar causes. When the general movements of respiration are hurried, those of the glottis are also accelerated; and when the movements of the chest are slower or fainter than usual, those of the glottis are diminished in the same proportion.

Fig. 55.



Human Larynx, viewed from above in its ordinary post-mortem condition.—*a.* Vocal chords. *b.* Thyroid cartilage. *c, c.* Arytenoid cartilages. *o.* Opening of the glottis.

Fig. 56.



The same, with the glottis opened by separation of the vocal chords.—*a.* Vocal chords. *b.* Thyroid cartilage. *c, c.* Arytenoid cartilages. *o.* Opening of the glottis.

In the glottis, as in the chest, the movement of inspiration is an active one, and that of expiration passive. In inspiration, the glottis is opened by contraction of the posterior crico-arytenoid muscles; which originate from the posterior surface of the cricoid cartilage, and, running thence upward and outward, are inserted into the external angles of the arytenoid cartilages. By these muscles, the arytenoid cartilages are rotated upon their articulations, so that the vocal chords, attached to their anterior extremities, are stretched and separated from each other. In this way, the orifice of the glottis may be nearly doubled, its area being increased from 0.94 to 1.69 square centimetre.

At the time of expiration, the posterior crico-arytenoid muscles are relaxed, the elasticity of the vocal chords replacing them in their former position.

The mechanism of respiration consists, therefore, of two sets of movements, those of the chest and those of the glottis. These movements, in the normal condition, correspond with each other both in time and intensity. It is at the same moment and by the same nervous influence, that the chest expands to inhale the air, while the glottis opens to admit it; and in expiration, the muscles of both chest and glottis are relaxed, while the elasticity of the tissues restores the parts to their original condition.

Rapidity of Respiration.—The movements of respiration in man follow each other for the most part with great regularity, and, according to the most extensive and varied observations, at the average rate of 20 inspirations per minute. This rate varies under different conditions, one of the most important of which is age. As a rule, respiration is more rapid in children than in adults. Quetelet has found the average rate in the newly born infant 44 per minute, and at the age of 5 years 26 per minute, being reduced between the ages of fifteen and twenty years, to the standard rapidity of 20 per minute. In the adult, according to the same observer, a condition of rest or activity readily influences the number of respirations; which are less frequent during sleep than in the waking condition. Even a difference in posture has a perceptible effect, the number of respirations in one individual being 19 per minute while lying down, and 22 per minute when standing up.* Any special muscular activity, as rapid walking or running, at once increases the frequency of respiration, which returns to its ordinary regularity soon after the exertion has ceased.

The movements of respiration are involuntary in character, and even their acceleration or diminution is mainly regulated by influences beyond our control. It is possible for a short time to increase or retard the rate of respiration, within certain limits, by voluntary effort; but this cannot be done continuously. If we intentionally arrest the breathing or diminish its frequency, after a short interval the nervous impulse becomes too strong to be controlled, and the movements recommence as usual. If on the other hand we purposely accelerate respiration to any great degree, the exertion soon becomes too fatiguing for continuance, and the movements return to their normal standard.

Quantity of Air used in Respiration.—Like all quantitative estimates connected with respiration, that of the inspired and expired air varies considerably as given by different observers. The peculiarities of individual constitution, as well as the conditions of rest and activity,

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*Milne-Edwards, Leçons sur la Physiologie. Paris, 1857, tome ii., p. 483.

prevent our arriving at an absolutely uniform standard. The average result, derived from several of the most trustworthy experimenters, as well as from our own observations, gives the amount of air taken into and expelled from the lungs with each respiration as 320 cubic centimetres. This estimate is certainly not above the reality. If we take, accordingly, eighteen respirations per minute as the mean rapidity between the sleeping and waking hours, this would amount to 5760 cubic centimetres of inspired air per minute, 345,600 per hour, and 8,294,400 cubic centimetres, or 8294.4 litres per day. But as the breathing is increased, both in rapidity and volume, by every muscular exertion, the daily quantity of air used in respiration is not less than 10,000 litres, or 350 cubic feet. This is 140 times the bulk of the entire body.

Estimates of this kind are sometimes used to calculate the air-space necessary for each inmate of a hospital or school-room. This alone, however, can never be sufficient for the purpose. The successful ventilation of a room depends not so much on the quantity of air which it contains as on that introduced and expelled within a certain period. The air of a small room, if properly renewed, may be amply sufficient for respiration, while that of a large room, if it remain stagnant, will become unfit for use. A large air-space will render ventilation more easy of accomplishment by ordinary methods, because the air will not be so rapidly vitiated as if it were in smaller volume; but it must still be changed with a rapidity proportionate to its contamination, in order to maintain the apartment in a wholesome condition.

Changes in the Air by Respiration.

The atmospheric air is a mixture of oxygen and nitrogen in the proportion, by volume, of about 21 parts of oxygen to 79 parts of nitrogen. It also contains .05 per cent. of carbonic acid, a varying quantity of watery vapor, and some traces of ammonia. The last named ingredients, so far as animal respiration is concerned, are insignificant in comparison with the oxygen and nitrogen which form the principal part of its mass.

As discharged from the lungs in expiration, the air is found to have become altered in the following particulars: first, it has lost oxygen; secondly, it has gained carbonic acid; and thirdly, it has absorbed the vapor of water. The most important of these changes are its diminution in oxygen and its increase in carbonic acid.

Diminution of Oxygen.—According to Valentin, Vierordt, and Regnault and Reiset, the air loses during respiration, in man, on an average, five per cent. of its volume of oxygen. At each inspiration, about 16 cubic centimetres of oxygen are removed from the air and absorbed by the blood; and, as the daily quantity of air used in respiration is about 10,000 litres, the oxygen consumed in twenty-four hours is not less than 500 litres, or seven times the bulk of the entire body.

This is, by weight, 715 grammes, or rather more than one pound and a half avoirdupois.

The absorption of oxygen by different animals varies according to their functional activity; and this difference exists even between those of the same class. In the sparrow the amount of oxygen absorbed, in proportion to the bodily weight, is ten times as great as in the common fowl; and in a carp the quantity consumed in an hour would hardly be sufficient for the respiration of a pigeon for a single minute.

In the same individual a temporary increase of muscular activity augments in a marked degree the absorption of oxygen. It was found by Lavoiser and Seguin that a man, who in the ordinary condition absorbed a little over 19,000 cubic centimetres of oxygen per hour, consumed nearly 13,000 cubic centimetres during fifteen minutes of active exercise; the rapidity of absorption being increased to more than 2½ times its former rate. On the other hand, the process is diminished in activity during sleep; and in hibernating animals, and in insects undergoing transformation, at the time of their most profound lethargy it is reduced to a mere vestige, as compared with their usual condition. Spallanzani observed that in insects the oxygen consumed in a given time by the chrysalis was far less than that absorbed by the caterpillar or the butterfly; and in the experiments of Regnault and Reiset on the marmot, the consumption of oxygen by this animal at the commencement of the cold season was about 500 cubic centimetres per hour for every kilogramme of bodily weight, while after hibernation was fully established it was reduced to 26 cubic centimetres per kilogramme per hour.

The absorption of oxygen, accordingly, in respiration, is directly associated, in rapidity and amount, with the physiological activity of the living organism.

Owing to its diminution in oxygen, air which has once been breathed is less capable of supporting respiration than before. When an animal is confined within a limited space, the air becomes poorer in oxygen as respiration goes on; and when its proportion has been reduced to a certain point, the animal dies, because a substance essential to life is no longer present in sufficient quantity. Different animals are affected in various degrees by a given diminution in the atmospheric oxygen. Cold-blooded species, in which respiration is comparatively slow, may still breathe when only a very small quantity of oxygen is present; and it has been found that electrical fishes, as well as slugs and snails, may continue respiration until they have completely exhausted the oxygen in the water or air in which they are confined. But where respiration is active, as in birds, quadrupeds, and man, a partial reduction of the oxygen is sufficient to cause death. If the carbonic acid exhaled be absorbed by an alkaline solution, so that the purity of the air be maintained, it is found that a sparrow dies in an hour when the proportion of oxygen has been reduced to 15 per cent.; and a mouse dies in five minutes when it is reduced to 10 per cent. ;[*] the remainder of the air in both cases consisting of nitrogen. In man asphyxia is almost immediately produced when the proportion of oxygen has fallen to 10 per cent.

As a candle flame is also extinguished in an atmosphere deprived of oxygen, this test is sometimes employed to determine whether it be safe to enter an atmosphere of doubtful composition. In bread-rooms and beer-vats, where fermentation has been going on, in wells which have been for a long time closed, or in old underground cavities or passages, the atmosphere is frequently so poor in oxygen that it would be unsafe to enter them without precaution. A lighted candle is, accordingly, let down into the suspected cavity, and if sufficient oxygen be present, it continues to burn; if not, it is extinguished.

This test is the more valuable, because the proportion of oxygen necessary for the combustion of a candle is greater than that required for the immediate support of respiration. A candle is extinguished when the air contains only 17 per cent. of its volume of oxygen, while less than this may still serve a short time for respiration. According to Milne-Edwards, a man may respire in an atmosphere which is insufficient to support combustion; and we have repeatedly seen pigeons continue to breathe in air in which a candle flame was immediately extinguished.

But although an atmosphere containing from 10 to 17 per cent. of oxygen is not at once fatal to man, it is still unfit for continued breathing, and after a time its deleterious effects would become manifest. A complete renewal of the deteriorated air, in such cases, is essential to the perfect performance of respiration.

Increase of Carbonic Acid.—The expired air usually contains, in man, about 4 per cent. of its volume of carbonic acid, which it has absorbed in the lungs. Rather less than 13 cubic centimetres of this gas are, therefore, given off with each ordinary expiration; and as 10,000 litres of air are inhaled and discharged during twenty-four hours, this will give 400 litres of carbonic acid as the amount expired per day. This quantity is, by weight, 786 grammes, or rather less than one pound and three-quarters avoirdupois.

The exhalation of carbonic acid by respiration varies, for the most part, in a similar way, with the absorption of oxygen. In general, it may be said, as the result of many trustworthy observations, both in animals and man, that the carbonic acid exhaled during a given time, is increased by muscular exertion, or any other physiological activity of the system, and is diminished by quietude, during sleep, and in a state of inanition.

These facts were first established, particularly for the human subject, by Scharling,[†] who found that the quantity of carbonic acid exhaled

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[*] Milne-Edwards, Leçons sur la Physiologie. Paris, 1857, tome ii., p. 638.

[†] Annales de Chimie et de Physique. Paris, 1843, tome viii., p. 490.

was greater during digestion than in the fasting condition; in the waking hours than during sleep; and in a state of activity than in one of repose. It was diminished by fatigue, and by most conditions which interfere with health.

In man the rate of exhalation also varies according to age, sex, constitution, and development. These variations were investigated by Andral and Gavarret, who found them very marked in different individuals, notwithstanding that the experiments were made at the same period of the day, and with the subject as nearly as possible in the same condition. The carbonic acid exhaled per hour in five different persons was as follows:

QUANTITY OF CARBONIC ACID PER HOUR.

In subject No. 1	19,770 cubic centimetres.
" " " 2	15,888 " "
" " " 3	20,475 " "
" " " 4	20,475 " "
" " " 5	26,060 " "

From eight years up to puberty the quantity of carbonic acid increases constantly with the age. Thus a boy of eight years exhales, on the average, 9238 cubic centimetres per hour; while a boy of fifteen exhales 16,168 cubic centimetres in the same time. Boys exhale during this period more carbonic acid than girls of the same age. In males the quantity of carbonic acid increases until the twenty-fifth or thirtieth year, when it reaches, on the average, 22,899 cubic centimetres per hour. It then remains stationary for ten or fifteen years; diminishes slightly from the fortieth to the sixtieth year; and after sixty shows a marked reduction, falling sometimes as low as 17,000 cubic centimetres. In one superannuated person, 102 years of age, the hourly quantity was less than 11,000 cubic centimetres.

In women, the increase of carbonic acid ceases at puberty; its production then remaining constant until the cessation of menstruation, about the fortieth or forty-fifth year. At that time it increases again until after fifty years, when it subsequently diminishes with the approach of old age, as in men. Pregnancy, occurring at any time in the above period, produces a temporary increase in the quantity of carbonic acid.

The strength of constitution, and particularly *the development of the muscular system*, has great influence in this respect. The largest production of carbonic acid observed was in a young man, 26 years of age, of remarkably vigorous and athletic development, who exhaled 26,060 cubic centimetres per hour. On the other hand, an unusually large skeleton, or an abundance of adipose tissue, is not accompanied by a corresponding increase in carbonic acid.

The discharge of carbonic acid is not altogether confined to the lungs, but takes place also, in some measure, by the urine and the perspiration. Morin* found that the urine always contains in solution certain gases, of which carbonic acid is the most abundant. The mean result of fifteen observations showed that urine excreted during the night contains about 1.96 per cent. of its volume of carbonic acid. During the day the quantity of this gas varies considerably, according to the condition of repose or activity; since after remaining quiet for an hour or two, it was only 1.19 per cent. of the volume of the urine, while after continued exertion for a similar period the urine was augmented in quantity, and its proportion of carbonic acid at the same time nearly doubled, amounting to 2.29 per cent. of its volume.

An equal or even greater activity of gaseous exhalation takes place by the skin. It has been found, by inclosing one of the limbs in an air-tight case, that the air in which it is confined loses oxygen and gains carbonic acid. From an experiment of this sort, Scharling estimated the carbonic acid given off from the whole cutaneous surface, in man, as from one-sixtieth to one-thirtieth of that discharged by the lungs. In the more recent observations of Aubert, the whole body without clothing, was confined in an air-tight case, leaving only the head exposed. Ventilation was kept up during the experiment with air free from carbonic acid, while the carbonic acid exhaled from the body was absorbed by baryta-water. Each observation lasted for two hours, and the average result obtained was that, for the entire day of twenty-four hours, 198 cubic centimetres of carbonic acid were exhaled from the skin; a quantity representing rather less than one two-hundredth of that given off by the lungs.

In the amphibious reptiles, as frogs, newts, and salamanders, which breathe by lungs, and yet can remain under water for a considerable time, the integument takes a more active part in respiration. The skin of these animals, which is thin, moist, and covered with a delicate epithelial layer, presents the most favorable conditions for gaseous transudation; and beneath the surface of the water, while the lungs are comparatively inactive, exhalation and absorption take place through the skin, and respiration goes on almost without interruption.

Indifference of Nitrogen in the Act of Respiration.—Notwithstanding the abundance of free nitrogen in the atmosphere, and its existence to some extent in the circulating fluids, this substance takes no direct part in respiration or nutrition. Even in vegetables, the nitrogen required for their albuminous ingredients is derived only from pre-existing nitrogenous compounds, mainly nitrates and ammonium salts. In animals, according to the conclusions generally accepted,† there is no satisfactory evidence that the free nitrogen of the air has any share in the phenomena of combination or decomposition within the body. It appears to serve as a vehicle or medium of admixture for the introduction of oxygen; remaining in other respects an indifferent substance in the respiratory process.

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* Journal de Pharmacie et de Chimie. Paris, 1864, tome xlv., p. 396.

† Hoppe-Seyler, Physiologische Chemie. Berlin, 1877, p. 48.

Discharge of Water in Respiration.—The water exhaled with the breath is given off by the pulmonary mucous membrane, by which it is absorbed from the blood. At ordinary temperatures it is a transparent, invisible vapor; but in cold weather it becomes partly condensed on leaving the lungs, and appears as a cloudy precipitate in the breath. According to Valentin, the average quantity exhaled from the lungs is about 500 grammes per day.

The exhalation of water by the lungs is a physical process, dependent on the moist and permeable structure of the pulmonary membrane and the vaporization of watery fluid at the ordinary pressure of the atmosphere. Any moist animal membrane, after death as well as during life, loses water by evaporation and becomes gradually desiccated. Experiments on recently killed frogs show that spontaneous desiccation goes on at first rapidly, and afterward more slowly, as the proportion of water in the tissues is diminished. In the lungs of a warm-blooded animal during life all the requisite conditions for rapid evaporation are present, namely, a moderately elevated temperature, a constant renewal of atmospheric air by the movements of respiration, and a continuous supply of moisture by the circulating blood. The watery vapor exhaled is therefore increased or diminished according to the rapidity of respiration, dryness or humidity of the atmosphere, and the activity of the pulmonary circulation.

In some animals, as in the dog, where the integument is comparatively deficient in perspiratory glands, the pulmonary transpiration becomes more active; and it is not uncommon for these animals, in hot weather, to lie at rest with their tongues protruded, and breathing from one hundred to two hundred times per minute, for the purpose of increasing the watery exhalation from the lungs.

In man the precise physiological value of the pulmonary transpiration is not known. Though varying according to the physical conditions above mentioned, it is a continuous process, and even at ordinary temperatures the expired breath received on a polished glass or metallic surface will produce an immediate dimness by the condensation of moisture. It is possible that the vapor thus exhaled, beside being complementary to the cutaneous perspiration, may also serve as a vehicle for the discharge of other substances.

Exhalation of Organic Matter by the Breath.—Beside carbonic acid and water, the expired air contains an organic ingredient, which communicates a faint but perceptible odor to the breath. This substance is discharged as an ingredient in the watery vapor of respiration. Under ordinary circumstances it is in so small quantity as to be hardly noticeable; but if a large number of persons remain for some hours in an apartment with insufficient ventilation, it accumulates in the atmosphere to such an extent that its odor becomes offensive. According to Carpenter, the watery fluid condensed from the expired air, if kept in a closed vessel at ordinary temperatures, exhales, after a time, a putrescent odor which could only come from decomposing organic substances.

When fresh and in the healthy condition, the organic ingredient of the expired breath is not offensive and appears to have no unwholesome qualities. It is only when accumulated in undue quantity, and allowed to stagnate in the atmosphere, that its disagreeable properties become manifest. It appears to be distinct in character for each species of animal; and as it is liable to be absorbed and retained by porous materials, such as wood, plaster, or woven fabrics, its odor remains perceptible in any small inclosure or transportation-car in which such animals have been confined. It has not been isolated in any case in sufficient quantity to determine its exact composition.

Vitiation of Air by Continued Respiration.—It appears from the foregoing that the air, when discharged in expiration, has been deteriorated by the loss of oxygen, and by the addition of matters derived from the lungs. Under ordinary conditions, the deteriorated air is at once diffused in the surrounding atmosphere, rising to a higher level on account of its increased temperature, and dispersed by the aerial currents; so that a fresh supply, of normal constitution, is taken into the lungs with each inspiration. But when breathing is carried on in a limited space, the air necessarily becomes vitiated; and this effect is produced with greater rapidity, the smaller the volume of the air and the larger the number of men or animals using it for respiration.

The vitiation of the air by respiration is, accordingly, the result of several changes taking place at the same time, and its effects are due to all these alterations combined.

So far as regards immediate danger to life, the *diminution of oxygen* is the most important change in the vitiated air, when carried to a sufficient extent. We have already seen that for man and mammalians, the air is completely irrespirable when its proportion of oxygen is diminished to 10 per cent. In these experiments, however, the exhaled carbonic acid was removed, as fast as produced, by the action of an alkaline solution, so that the air remained in a state of purity except for its loss of oxygen. But if the products of respiration be allowed to accumulate at the same time, the loss of oxygen is more quickly felt. In the experiments of Leblanc, a dog and a pigeon, breathing in a confined space, were both reduced to extremities when the air was contaminated with 30 per cent. of carbonic acid, though still containing 16 per cent. of oxygen.

The second element in the vitiation of the respired air is the presence of *carbonic acid.* The effect of this gas, as produced by respiration, cannot be ascertained from that of carbonic acid alone. A man or an animal, suddenly introduced into an atmosphere of pure carbonic acid, dies at once by suffocation. But this result is not caused by the influence of carbonic acid. It is due to the absence of oxygen; and death would take place as promptly in an atmosphere of nitrogen or any other indifferent gas. It may be said that, in general, for birds and small mammalians, the atmosphere becomes incapable of supporting life when, in addition to its normal proportion of oxygen, it contains 20 per cent. of carbonic acid; that is, five times as much as is present, in man, in the expired breath. But Regnault and Reiset found that dogs and rabbits could continue to breathe without difficulty in an atmosphere containing even 23 per cent. of carbonic acid, provided its oxygen were increased to 30 or 40 per cent. Thus a part, at least, of the influence of carbonic acid, when in large quantity, is due to its action in excluding or interfering with the absorption of oxygen.

Pure carbonic acid, mixed with atmospheric air of normal constitution, is not so fatal in its effect as sometimes represented. If a pigeon be confined in a glass receiver with a wide open mouth, and carbonic acid be introduced through a tube placed just within the edge of the vessel, so that it will gradually mingle with the air, it produces rapid and laborious respiration, gradually increasing in intensity; and in a few moments the animal falls in a state of insensibility. But if the receiver be removed, allowing the free access of fresh air, the insensibility soon passes off, and in a few moments the animal is again breathing in a natural manner, without having suffered any permanent injury. The action of carbonic acid, administered in this way, is similar to that of an anæsthetic vapor, like ether or chloroform, with the addition of strong symptoms of dyspnœa.

In man the immediate effects of carbonic acid in the inspired air are of a similar nature. The inhalation of pure carbonic acid from a gasometer is at first extremely difficult, as its stimulating effect on the mucous membrane produces spasmodic stricture of the glottis. If the gas, however, be allowed to remain for a short time in contact with the mucous membrane this effect passes off, the glottis may be gently opened, and the carbonic acid drawn into the lungs, by a deep inspiration, to the amount of from 800 to 1200 cubic centimetres. At first it produces only a sensation of warmth and moderate stimulus in the chest. But at the end of two or three seconds there comes on very suddenly a sense of extreme dyspnœa, with rapid and laborious respiration, followed by dimness of vision, slight confusion of mind, and partial insensibility, all of which symptoms soon disappear, as respiration returns to its normal condition, leaving a feeling of quietude and tendency to sleep.

Notwithstanding, however, the intense feeling of dyspnœa produced by such an inhalation, the external signs of suffocation are very slight, and bear no proportion to the severity of the sensations. They are confined to a little suffusion of the face, with partial lividity of the lips; and the pulse is but little if at all affected.

A mixture of carbonic acid and atmospheric air in equal volumes produces a perceptible feeling of warmth and pungency at the glottis, but may still be readily drawn into the lungs. After two or three deep inspirations, the strong sense of want of air, with rapid and laborious respiration, comes on as before. The dyspnœa, suffusion of face, and lividity are less marked than after breathing the pure gas, but the subsequent condition of quiescence and partial anæsthesia, is more decided and of longer continuance.

A mixture of one volume of carbonic acid with three volumes of atmospheric air may be inspired without difficulty, producing a rather agreeable sensation in the lungs. After about 3000 cubic centimetres have been inhaled in successive inspirations, a sense of dyspnœa comes on, which, however, is not particularly increased by continuing the inspiration to 6000 cubic centimetres. The nervous symptoms are moderate in degree, but similar to the preceding.

On the other hand, pure nitrogen has no taste nor odor, nor does it have any stimulating effect on the mucous membrane. It may be inspired to the amount of 6000 cubic centimetres, without producing any sense of dyspnœa, or any perceptible effect on the nervous system.

These results indicate that the presence of carbonic acid in the lungs acts as a stimulus to respiration by causing a sense of the want of air; and that, furthermore, its principal toxic effect, when in abnormal quantity, is the production of more or less insensibility or anæsthesia. The sense of drowsiness and inattention experienced in an imperfectly ventilated lecture-room or theatre is probably due to this cause, especially as the burning gas-lights contribute at the same time to the formation of carbonic acid. The temporary nature of these sensations, and their immediate relief on coming into the open air, are matters of common observation.

The third element in the vitiation of air by the breath is the exhalation of *organic vapor.* This is the least understood, but probably the most deleterious ingredient of the atmosphere produced by respiration. It is this which causes the offensive odor, and the sense of oppression on entering any confined space, where too great a number of persons have remained without sufficient renewal of the air. It is most marked when continued respiration, with neglect of ventilation, has been going on over night, as in a crowded dormitory or sleeping-car; since the organic emanations have then had time not only to accumulate but also to pass into a state of incipient decomposition. In this condition they resemble the class of animal poisons; and there is reason to believe, that when introduced into the system, they may cause disturbances which last for a considerable time. It is certain that the contagion of many febrile diseases is communicated through the air by the products of respiration; and the normal organic exhalations of the pulmonary mucous membrane, when altered by concentration, the accumulation of moisture, and an elevated temperature are perhaps capable of producing analogous effects.

All the above causes of vitiation of the atmosphere in respiration, notwithstanding the differences in their nature and effects, are to be obviated by the same means; that is, a sufficient renewal of the air by ventilation.

Relation between the Oxygen absorbed in Respiration and the Carbonic Acid given off.—It has been seen that, in man, with each respiration, on the average, 16 cubic centimetres of oxygen are absorbed, and 13 cubic centimetres of carbonic acid given off. As the oxygen thus taken in weighs rather less than .023 gramme while the carbonic acid discharged weighs

.025 gramme, it is evident that the gross result is a loss of weight to the system, and this loss, by continued respiration, amounts on the average to a little over 70 grammes per day. This is one of the most important facts connected with respiration. It shows that this function is carried on at the expense of the bodily substance, since the oxygen and carbon discharged under the form of carbonic acid weigh more than the oxygen absorbed in a free state. The difference must accordingly be supplied in some way by the food; and if this be withheld, respiration alone will be sufficient to diminish gradually the weight of the body, and to bring it at last to a state of emaciation.

If we endeavor to ascertain what becomes of the inspired oxygen, it appears, in the first place, that the quantity of this gas which disappears from the air is not entirely replaced in the carbonic acid of the breath; that is, there is less oxygen in the carbonic acid returned to the air by expiration than has been taken from it by inspiration.

The proportion of oxygen which disappears in the body, over and above that returned by the breath as carbonic acid, varies in different animals. In the herbivora it is about 10 per cent. of the oxygen inspired; in the carnivora, 20 or 25 per cent.; and even in the same animal, the proportion of oxygen absorbed, to that of carbonic acid exhaled, varies according to the food upon which he subsists. In dogs fed on meat, according to Regnault and Reiset,* 25 per cent. of the inspired oxygen disappears in the body of the animal; but when fed on starchy substances, all but 8 per cent. reappears in the expired carbonic acid. Under some conditions, there may be a difference in the opposite direction; that is, more oxygen may be contained in the carbonic acid exhaled than is absorbed in a free state from the atmosphere. In some of the experiments of Regnault and Reiset, with rabbits and fowls fed exclusively on bread and grain, the oxygen in the expired carbonic acid was 101 or 102 per cent. of that taken in by respiration; and even in man, according to Doyère, the quantity of oxygen discharged as carbonic acid, may be considerably greater than that absorbed. But in general it is the reverse; the quantity of oxygen not accounted for in the expired carbonic acid being habitually greater in the carnivorous animals than in the herbivora.

These facts have been established by direct observation, without reference to the supposed manner in which the internal changes of respiration take place. Nevertheless, they are susceptible of so ready an explanation that there can be little doubt of their significance. The simplest case would be that of an herbivorous animal living exclusively on carbo-hydrates, as starch or sugar. Since these substances already contain oxygen and hydrogen in the proportions to form water, any further oxidation must result in the production of carbonic acid; and in this case the same quantity of oxygen as that taken in must be returned to the atmosphere as a constituent of the carbonic acid exhaled: the remainder of the carbo-hydrate being separated in the form of water. This process is represented in the following formula:

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* Annales de Chimie et de Physique. Paris, 1849, tome xxvi., pp. 409–451.

$$\underset{\text{Starch.}}{C_6H_{10}O_5} + O_{12} = \underset{\text{Carbonic acid.}}{6(CO_2)} + \underset{\text{Water.}}{5(H_2O)}.$$

In an animal supported on this food, the whole of the oxygen taken in by respiration would reappear in the expired carbonic acid. But in an animal also consuming fatty substances, the proportions would be changed. As these matters do not contain enough oxygen to form water with their hydrogen, more oxygen must be taken in with the breath than is needed to convert their carbon into carbonic acid; and a part of it will consequently disappear from the gaseous products of respiration. The change in this instance is as follows:

$$\underset{\text{Oleine.}}{C_{57}H_{104}O_6} + O_{160} = \underset{\text{Carbonic acid.}}{57(CO_2)} + \underset{\text{Water.}}{52(H_2O)}.$$

In effecting, therefore, the complete disappearance of a fatty substance, 160 parts of oxygen will be absorbed, and only 114 parts returned in the carbonic acid. This will also take place where albuminous matters are used as food, since all the nitrogen of these substances is excreted in the form of urea; and after the separation of urea from albumen, what is left must be analogous in composition to fat; that is, containing less oxygen than would be required to convert its hydrogen into water.

It is no doubt for these reasons that, in herbivorous animals, feeding largely on carbo-hydrates, the oxygen exhaled in the carbonic acid is nearly equal to that taken in with the breath; while in carnivora, which consume only fats and albuminous matters, a larger proportion of oxygen disappears from the products of respiration.

Finally, some kinds of vegetable food, as fruits and green tissues, contain substances, the oxygen of which is more than sufficient to form water with their hydrogen. Such are the salts of vegetable acids, like oxalic, citric, gallic, malic, and tartaric acid. The result of the internal consumption of tartaric acid, for example, would be as follows:

$$\underset{\text{Tartaric acid.}}{C_4H_6O_6} + O_5 = \underset{\text{Carbonic acid.}}{4(CO_2)} + \underset{\text{Water.}}{3(H_2O)}.$$

In this instance more oxygen will be exhaled, in the carbonic acid produced, than was absorbed from the atmosphere; because a superabundance already existed in the material used as food.

The proportions of oxygen and carbonic acid, absorbed and expired in respiration, will therefore vary, as shown by Mayer,* not only with the nature of the food, but also according to the transformations, within the living organism, of one nutritive substance into another, as of a carbohydrate into a fat, or of either into an organic acid. In the fermentation of glucose (p. 57) there is even an elimination of carbonic acid without any absorption of oxygen whatever; this being a process, not of direct oxidation, but of the rearrangement of elements already present in the sugar, a portion being exhaled as carbonic acid, while the rest remain in the form of alcohol.

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* Lehrbuch der Agrikultur-Chemie. Heidelberg, 1871, p. 101.

Changes in the Blood by Respiration.

The blood as it circulates in the arterial system has a bright scarlet color; but in passing through the capillaries it gradually becomes darker, and on arriving in the veins it is deep purple, or in some situations nearly black. There are, therefore, two kinds of blood in the body; arterial blood, which is of a bright color, and venous blood, which is dark. The dark colored venous blood is incapable, in this state, of supplying the organs with their normal stimulus and nutrition, and has thus far lost its value as a circulating fluid. It is accordingly returned to the heart by the veins, and is thence sent, through the pulmonary artery, to the lungs. In passing through the pulmonary circulation it reassumes its scarlet hue, and is again converted into arterial blood. Thus the most striking physical effect produced in the blood by respiration is its change of color from venous to arterial.

This change is effected by the air in the pulmonary cavities. If defibrinated blood, recently drawn from the veins, be shaken up with atmospheric air, it at once changes its color and acquires the bright hue of arterial blood. If forced by injection through the blood-vessels of the inflated lungs, it exhibits the same change. In a dog, or other mammalian, if the thorax be opened, and artificial respiration kept up by the nozzle of a bellows inserted into the trachea, the dark venous blood can be seen in the great veins and in the right auricle of the heart, while that returning from the lungs to the left auricle is bright red. If respiration be suspended, the blood soon ceases to be arterialized in the lungs, and returns to the left auricle of a dark venous hue. On recommencing respiration, the blood is again arterialized, its red color reappearing in the pulmonary veins and the left cavities of the heart.

Simultaneously with its alteration of color during the pulmonary circulation, the blood undergoes a change in its gaseous constituents, the converse of that which is produced in the air; that is, it absorbs oxygen and exhales carbonic acid.

Passage of Oxygen into the Blood in Respiration.—The oxygen which disappears from the air in the lungs is taken up by the blood in the pulmonary capillaries. It does not enter into immediate chemical union with the organic ingredients present, but remains in such loose combination that it may be removed from the blood by the air-pump, or by a current of hydrogen or nitrogen, and especially by the action of carbonic oxide (C O), which expels it completely. According to a large number of observations, its quantity, in the arterial blood of the dog, may vary from a little over 10 per cent. to 22 per cent. by volume; the average, in the experiments of Schoeffer and Ludwig,* being about 15 per cent.

Nearly the whole of the oxygen thus taken up is absorbed by the *red globules;* which have a special capacity in this respect, due to their hemoglobine. This is shown by the fact that the absorbent

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* Archiv für die gesammte Physiologie. Bonn, 1868, Band i., p. 279.

capacity of the blood for oxygen depends on the presence or absence of the red globules. According to Magnus, while the blood contains more than twice as much oxygen as water could hold in solution at the same temperature, the serum alone has no more solvent power for this gas than pure water; and on the other hand, defibrinated blood, that is, the serum and globules mingled, dissolves as much oxygen as the fresh blood. Pflüger found, as the average of six observations on the arterial blood of the dog, that the oxygen in the entire blood was, by volume, 15.6 per cent., while in the serum alone there was only 0.2 per cent. According to the same observer, the arterial blood in the carotid contains nearly though not quite all the oxygen which it is capable of holding in solution; since a specimen of dog's blood drawn directly from the artery contained 18.8 per cent. of oxygen, which was only increased to a little less than 20 per cent. by agitation with atmospheric air. The blood, therefore, either does not become fully saturated with oxygen in passing through the lungs, or else a little of this gas has already passed into some other combination before reaching the carotid arteries.

The color of the blood depends *on the presence or absence of oxygen*, not on that of carbonic acid. Venous blood, shaken up with oxygen or atmospheric air, at once assumes the arterial tint, though its carbonic acid may remain. According to Pflüger if defibrinated dog's blood be placed in two flasks, and shaken up, one with pure oxygen, the other with a mixture of oxygen and carbonic acid, both specimens will present the same bright color; both of them being found on analysis to contain nearly the same quantity of oxygen, while their proportions of carbonic acid are different. If blood be drawn after the animals have been made to breathe pure oxygen, or oxygen and carbonic acid mingled, it is of the same color in each instance; its percentage of oxygen being the same, while that of carbonic acid is different in the two cases.

It is the oxygen, therefore, which, on being taken up by the blood-globules, changes their color from dark purple to bright red. It passes off with the arterial blood in this condition, and is then distributed to the capillary circulation. Here, as the blood comes in contact with the tissues, its oxygen in great measure disappears, and its color is again changed from arterial to venous.

The loss of oxygen in the capillaries of the general circulation, is due to its transfer from the blood-globules to the tissues. Nearly all the tissues exert an absorbent power upon oxygen, when exposed to this gas or to atmospheric air. The experiments of Paul Bert* have shown that the fresh tissues, taken from the body of the recently killed animal and exposed to the air in closed vessels, absorb oxygen with different degrees of intensity, in the following order, namely: muscles, brain, kidneys, spleen, testicle, and pounded bones. Of these the muscles are the most active, absorbing 50 cubic centimetres of

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* Leçons sur la Physiologie comparée de la Respiration. Paris, 1870, p. 46.

oxygen for every one hundred grammes of muscular tissue; while the bones absorb only a little over 17 cubic centimetres for the same weight.

The absorbent capacity of the tissues for oxygen is even greater than that of the blood. This was shown by the experiments of Spallanzani, and more recently by those of Bert. In Bert's experiments, three equal portions of recently drawn defibrinated dog's blood were placed in test-tubes, a piece of fresh muscular tissue from the same animal being added to one of them, a portion of the spleen-tissue to another, and the third left to itself. After a time it was found that the tissues had abstracted oxygen from the blood with which they were in contact, so that in these two specimens the quantity of oxygen remaining was less than in the third, as follows:

QUANTITY OF OXYGEN BY VOLUME REMAINING IN	
Blood left to itself	18 per cent.
Blood containing spleen tissue	12 "
Blood containing muscular tissue . . .	6 "

Finally, successive analyses of the blood, as it passes from the arteries to the veins, show that its loss of oxygen is mainly in the capillary circulation. In general, according to Pflüger, the quantity of oxygen, by volume, in arterial blood is 15.6 per cent.; in venous blood 8 per cent.; that is, it is reduced about one-half in the capillaries of the general circulation. But in the blood of the hepatic veins, which has passed through a double set of capillary vessels, the loss of oxygen is much greater. Bernard* found that in the same dog, blood from different parts of the circulatory system, yielded the following quantities of oxygen:

QUANTITY OF OXYGEN BY VOLUME IN	
Arterial blood	18.93 per cent.
Venous blood from right side of heart . .	9.93 "
Venous blood from hepatic veins . . .	2.80 "

Thus the blood-globules serve as carriers of oxygen from the lungs where it is absorbed, to the tissues where it is consumed; the first object of respiration being to supply oxygen to the blood, in order that the blood may supply it to the tissues.

Exhalation of Carbonic Acid by the Blood.—The venous blood, as it returns to the heart, is charged with carbonic acid to such an extent that a portion of this gas is exhaled through the pulmonary membrane, and discharged with the breath. Its quantity in the blood has not been determined with the same accuracy as that of oxygen. Carbonic oxide, which is so efficient for the extraction of oxygen from the blood, displaces only a portion of its carbonic acid; and in the experiments of Bernard, the maximum quantity of carbonic acid obtained from venous blood by this means was only about 6.5 per cent. A much larger proportion may be extracted by the mercurial air-pump, amounting on the average, in the experiments of Ludwig, to about 28

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* Liquides de l'Organisme. Paris, 1859, tome i., p. 394.

per cent. for arterial blood, and about 31 per cent. for venous blood. But a large part of the carbonic acid obtainable in this way does not exist in the blood in a free form, but in combination with the alkaline carbonates of the plasma; since a watery solution of sodium bicarbonate will lose a portion of its carbonic acid, and become reduced to a carbonate by being subjected to a vacuum, or even by agitation with hydrogen at the temperature of the body. Lehmann* found that after the expulsion from ox's blood of all the carbonic acid removable by the air-pump and a current of hydrogen, there still remained 0.1628 per cent. of sodium carbonate, with which a certain quantity of the carbonic acid previously given off must have been united in the form of bicarbonate.

It is estimated by Bert, from the experiments of Fernet, that a portion of the carbonic acid of the blood is in simple solution, and a portion combined with the alkaline salts; the blood, when artificially saturated with this gas, containing about three-fifths in a state of solution, and about two-fifths in a state of combination. We do not know, however, what this proportion is in the living body; and the large amount of carbonic acid removable by a vacuum does not represent accurately that which is capable of exhalation through the pulmonary membrane. This quantity is very much smaller. We know that, on the average, 13 cubic centimetres of carbonic acid are discharged from the lungs, in man, with each expiration; and during this interval, judging from the capacity of the heart, and its frequency of pulsation, there can hardly be less than 400 cubic centimetres of blood, passing through the pulmonary circulation. This would give only a little over three per cent. as the volume of carbonic acid discharged from a given quantity of blood in respiration. The average results obtained by extraction with the mercurial air-pump, in the experiments of Ludwig, give this quantity as the actual difference between venous and arterial blood, as follows:

AVERAGE QUANTITY OF CARBONIC ACID REMOVABLE BY THE AIR-PUMP, FROM

Venous blood	31.27 per cent.
Arterial blood	27.99 "
Difference	3.28 "

All the different modes of analysis, whether by carbonic oxide, indifferent gases, or the air-pump, though differing in the quantity extracted, show that there is less carbonic acid in arterial than in venous blood, and accordingly that this gas is exhaled from the circulating fluid during its passage through the lungs.

Unlike oxygen, the carbonic acid of the blood is principally contained in the *plasma*, and not in the globules; since the serum has nearly the same capacity of absorption for this gas as the entire blood.

Source of the Carbonic Acid of the Blood.—The source of the carbonic acid of the blood, as well as the destination of its oxygen, is in

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* Physiological Chemistry, Cavendish edition. London, 1854, vol. i., p. 438.

the tissues. Every organized tissue, in the recent condition, has the power both of absorbing oxygen and of exhaling carbonic acid. G. Liebig showed that frogs' muscles, recently prepared and freed from blood, will absorb oxygen and discharge carbonic acid. Similar experiments with other tissues have led to the same result. It is in their substance, accordingly, that the oxygen is consumed, and the carbonic acid takes its origin. But these two phenomena are not immediately dependent on each other. In some instances, living animals as well as fresh animal tissues will continue, for a time, to exhale carbonic acid in an atmosphere of hydrogen or of nitrogen, or even in an exhausted receiver. Marchand found that frogs would live from half an hour to an hour in pure hydrogen; and that during this time they exhaled even more carbonic acid than in atmospheric air, owing probably to the superior displacing power of hydrogen for this gas. While 1000 grammes' weight of frogs exhaled about 0.077 gramme of carbonic acid per hour in atmospheric air, they exhaled during the same time in pure hydrogen as much as 0.263 gramme. The same observer found that frogs would recover after having remained for about half an hour in a nearly complete vacuum; and that, when killed by the total abstraction of air, 1000 grammes' weight of the animals had eliminated 0.600 gramme of carbonic acid. Similar facts were observed by Spallanzani; and Paul Bert* found that while a certain quantity of fresh muscular tissue, in atmospheric air, exhaled, in a given time, 30 cubic centimetres of carbonic acid, the same quantity, in pure hydrogen exhaled 23 cubic centimetres during the same time. He even found that the exhalation of carbonic acid would continue, in an atmosphere of nitrogen, from muscular tissue which had previously been subjected for a quarter of an hour to the action of a vacuum.

It is, furthermore, evident that in this internal process, as in the external phenomena of respiration by the lungs, the quantities of oxygen absorbed and of carbonic acid exhaled are not always in the same relation. Thus in the experiments of Bert on the gases absorbed and discharged by the tissues, in some instances the volume of carbonic acid produced was greater, and in others less than that of the oxygen consumed; the proportions of the two varying considerably in different cases.

The following list gives the result of a series of these experiments:

QUANTITY OF O AND CO_2 ABSORBED AND EXHALED DURING 24 HOURS, IN CUBIC CENTIMETRES.

By 100 grammes of	Oxygen absorbed.	Carbonic acid exhaled.
Muscle	50.8	56.8
Brain	45.8	42.8
Kidneys	37.0	15.6
Spleen	27.3	15.4
Testicles	18.3	27.5
Pounded bones . . .	17.2	8.1

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* Leçons sur la Physiologie comparée de la Respiration. Paris, 1870, p. 49.

The production of carbonic acid by the tissues is not, therefore, an immediate result of the absorption of oxygen. The precise mode in which carbonic acid originates in the solid organs is unknown; but it is probably by some decomposition in which a portion of the carbon and oxygen separate from their previous combinations in this form, while the remaining elements unite to produce other substances of different composition.

The most palpable phenomena of respiration consist, accordingly, in an interchange of gases between the blood and the lungs. As the blood on its return to the lungs is comparatively poor in oxygen and abundant in carbonic acid, it absorbs the former gas from the pulmonary cavity, and discharges the latter with the expired air. These changes, however, are incomplete, both in the air and in the blood. The expired air has never lost the whole of its oxygen, and it contains only about 4 per cent. of carbonic acid. On the other hand, venous blood still contains a moderate percentage of oxygen; and a certain quantity of carbonic acid is also present in arterial blood. It is only the proportion of these gases which is changed in respiration, the carbonic acid of the blood being diminished, and its oxygen increased, during its passage through the lungs.

The office of the respiratory apparatus is to afford ingress and egress to oxygen and carbonic acid, two substances which enter and leave the body in the gaseous form, but which have no immediate relation with each other, excepting that they are absorbed and exhaled by the same organs. They represent the beginning and the end of a series of internal changes, which are among the most important of those connected with the maintenance of life.

Nature of Respiration.—If we regard respiration in its gross results we must consider it as a process of oxidation. The living body absorbs, on the one hand, free oxygen from the atmosphere, and, on the other, takes into the alimentary canal organic substances as ingredients of the food. These organic substances, after performing their office in the system, are discharged from it partly under the form of urea, but mainly as carbonic acid and water. The final products of excretion represent the organic elements of the food, *plus* the oxygen which has been absorbed; and they return to the inorganic world in a condition of complete or nearly complete oxidation. These facts are incontestible, and they show plainly the general relations of the incoming and outgoing materials of the animal frame.

But when we endeavor to learn the place and manner of this oxidation in the living body, the attempt fails. There is no evidence of such direct action taking place in the circulating fluid, nor in any of the organs or tissues. The food in the alimentary canal, during digestion, undergoes catalytic transformations and solutions, but no oxidation; and it is absorbed from the intestine with its organic characters unimpaired. In the lungs the process of respiration consists in the absorption of oxygen and exhalation of carbonic acid. These two gases pass each other in the pulmonary cavities, on their way to and from the blood; neither of them being produced or consumed in these organs.

In the blood, the plasma consists mainly of organic substances in solution, and oxygen is abundant in the globules in a state of loose combination. But the union of the two certainly does not take place in the blood. Oxygen disappears from it in the capillary circulation, and is replaced by carbonic acid derived from the tissues. According to the view now generally accepted, the functions performed by the blood are rather physical than chemical in their nature. It is a vehicle of transportation for nutritious matters from the alimentary canal to various organs, and for oxygen and carbonic acid between the tissues and the lungs. It collects or disseminates substances which have already been prepared in other parts, and, as a general rule, conveys them unchanged to their destinations. Even a substance like pyrogallic acid, so readily oxidizable in an alkaline solution that it is employed for the quantitative determination of oxygen in the air, when introduced into the animal system passes through it without alteration, and reappears in the urine.* There is no evidence that the blood exerts anywhere a direct oxidizing action.

Finally, in the substance of the tissues and organs, it is evident that the carbonic acid which they produce is not the immediate result of the absorption of oxygen. Its continued exhalation in an atmosphere of nitrogen, or of other indifferent gases, shows that it originates, in all probability, by a separation of its elements from other previously existing forms of combination. Furthermore, the alteration of the organic ingredients, so far as we can follow them in the living body, consists largely of hydrations and dehydrations under the influence of the animal ferments. Glucose, when absorbed from the alimentary canal, is reduced, by dehydration in the liver, to the form of glycogen, which, in turn, is again converted by hydration into soluble glucose. The formation of glycocholic from taurocholic acid (p. 109) is a dehydration with elimination of sulphur, while biliverdine is produced from bilirubine (p. 101) by hydration with oxidation. On the other hand, the derivation of urobiline from bilirubine (p. 102) can only be accomplished by a reduction process; and the formation of fat in the body from carbohydrates (p. 63) is undoubtedly accompanied by the elimination of carbonic acid and the production of other substances at the same time.

From all these facts it appears that the transformation of tissue in the body is not a simple act of combustion, regulated by the supply of oxygen to the lungs. It is one in which the tissues appropriate the oxygen conveyed to them by the blood, to form intermediate compounds, and in which they finally eliminate carbonic acid as the most abundant product of their retrograde metamorphosis.

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* Gorup-Besanez. Lehrbuch der Physiologischen Chemie. Braunschweig, 1878, p. 599. Ewald. Die Lehre von der Verdauung. Berlin, 1879, p. 5.

CHAPTER V.

ANIMAL HEAT.

ONE of the characteristic properties of living creatures is that of maintaining, more or less constantly, a standard temperature, notwithstanding the external changes of heat or cold to which they are subjected. If a bar of iron or a vessel of water be heated to a temperature above that of the surrounding air, and then left to itself, it will at once begin to lose heat by radiation and conduction; and this loss will continue until, after a time, its temperature is reduced to that of the atmosphere. It then remains stationary at this point, unless the atmosphere should become warmer or cooler; in which case a similar change takes place in the inorganic body, its temperature varying with that of the surrounding medium.

With man and animals the case is different. If a thermometer be introduced into the rectum, or placed under the tongue, it will indicate in man a temperature of from 37° to 38° C. (about 100° F.),* whether the surrounding atmosphere be warm or cool. This internal bodily temperature is sensibly the same in summer and in winter. Although the external air may be at the freezing point, the internal parts of the body, when examined by the thermometer, will indicate their usual standard of warmth; and in ordinary summer weather the temperature of the air is, for the most part, many degrees below that of the living body. As the body, however, by exposure to such an atmosphere must be constantly losing heat by radiation and conduction, and yet maintains a standard temperature, it is plain that a certain amount of heat must be generated in its interior, sufficient to compensate for the external loss. The internal heat, so produced, is known by the name of *animal heat.*

Thus it is by its own internal heat that the body is warmed. The clothing used by man, and the fur, wool, or feathers by which animals are protected, have no warmth in themselves; they simply prevent the body from losing heat too rapidly, and thus becoming cooled down below its normal standard. Even the furnaces and fires of a dwelling house only serve to moderate the cooling influence of the air; for the atmosphere, even in the warmest apartment, never rises to the heat of the living body, which is still the only source of its own vital temperature.

Difference of Temperature in Different Classes of Animals.—The

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* To convert degrees of the Centigrade scale into the corresponding value for the Fahrenheit scale, multiply by 1.8 and add 32 to the product.

production of internal heat varies in intensity in different classes of animals. As a rule, it is most active in birds, whose temperature is in general 45° C. In mammalians it is 37° to 40°; and in man about 37.5°. As in these two classes the internal organs and the blood are nearly always above the temperature of the air or that of the skin, and, accordingly, feel warm to the touch, they are called "warm-blooded animals." In reptiles and fish, on the other hand, the production of heat is much less rapid, and preponderates so little over that of the air or water which they inhabit, that no marked difference is perceptible on cursory examination; and as their internal organs have a lower temperature than our own integument, and consequently feel cool to the touch, they are called "cold-blooded animals." This difference, however, is only in degree and not in kind. Reptiles and fish also generate a certain amount of heat, which may be measured by the thermometer. The temperature of frogs, serpents, tortoises, water-lizards, and fish has been found to be from 1.7° to 4.5° above that of the surrounding air or water.

In invertebrate animals the heat produced is usually still less perceptible because, from the greater surface of their bodies in proportion to their mass, the warmth is more rapidly dissipated. But when many of them are collected in a small space, and especially when in a state of activity, their heat is distinguishable by thermometric measurement. The temperature of the butterfly after active motion has been found from 2.77° to 5° above that of the air; that of the humble-bee from 1.5° to 5.5° higher than the exterior. According to Newport, the interior of a hive of bees may have a temperature of 9° with the external atmosphere at 1.4°, even while the insects are quiet; but if they be excited by tapping on the hive, it may rise to 38.8°. Thus so long as the insects are at rest, the thermometer indicates a very moderate warmth; but if kept for a few moments in rapid motion in a confined space, they may generate sufficient heat to produce a sensible elevation of temperature.

The production of heat is not confined to animals, but takes place also in vegetables. In vegetables, however, it is very rapidly lost, owing to the extensive surface presented by their ramifications and foliage, and the abundant evaporation of moisture. If this loss be diminished by keeping the air charged with watery vapor and thus preventing evaporation, the elevation of temperature becomes sensible and may be measured. Dutrochet* demonstrated, by the use of the thermo-electric needle, that nearly all parts of a living plant, such as the green stems, the leaves, the buds, and even the roots and fruit, generate heat to some degree; the maximum temperature thus reached being about 0.28° above that of the surrounding atmosphere. Subsequent observations have shown that in certain periods of vegetative activity, as in those of germination and flowering, the development

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* Annales des Sciences naturelles. Paris, 2me Série, tome xii., p. 277.

of heat is much more rapid. In the malting of barley, when a considerable quantity of germinating grain is piled in a mass, its elevation of temperature may be distinguished, both by the hand and the thermometer. The most abundant heat-production by vegetables is in the flowers of the Araceæ (Calla, Indian turnip, Sweet flag) at the time of fecundation,* which sometimes show a temperature of from 5° to 10° above that of the surrounding air.

The generation of heat is, accordingly, a phenomenon common to all living organisms. When the mass of the body is large in proportion to its extent of surface, its heat is readily perceptible both by the touch and by the thermometer. In birds and mammalians the heat production is more active than in reptiles and fish; and even in different species of the same class, it differs in degree according to the special organization of the animal and the general activity of its functions.

Quantity of Heat in the Living Body.—The quantity of heat produced in the body within a given time is measured by the increase of temperature which it produces in a known volume of water. Draper† found that the human body, with a volume of about 85 litres (3 cubic feet) and a weight of 81.65 kilogrammes (180 pounds avoirdupois), by remaining in the bath for one hour, could raise the temperature of 212 kilogrammes of water 1.11°; which he estimates, assuming the specific heat of the body to be about the same with that of water, would be capable of warming the body itself 2.77°. But as the temperature of the body, in the observation quoted, was lowered 0.55° while in the bath, the heat actually generated would be capable of warming the body, or an equal volume of water, 2.22°. This would be equivalent to 188.7 heat units,‡ produced by the human body in the course of one hour, or 2.31 heat units for every kilogramme of bodily weight.

In the experiments of Senator § on the heat-producing power in dogs, the animals were inclosed in a copper cage, through which ventilation was kept up at a known rate, the temperature of the incoming and outgoing air being noted at short intervals. The cage was surrounded by a known volume of water, at from 26.5° to 29° C., and the whole apparatus inclosed in an outer case made as non-conducting as possible; the heat actually lost from it being determined by preliminary observation. The internal temperature of the animal having been taken, he was introduced into the cage and allowed to remain for a certain time. The heat produced was ascertained by the increase of temperature in the water surrounding the cage, the result being corrected by that of the air used for ventilation, as well as by the variation in

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* Sachs, Traité de Botanique. Paris, 1874, p. 847.

† American Journal of Science and Arts. New Haven, 1872, vol. ii., p. 445.

‡ A *heat unit* is the quantity of heat required to raise the temperature of one kilogramme of water from 0° to 1° of the Centigrade scale.

§ Archiv für Anatomie, Physiologie, und wissenschaftliche Medicin. Leipzig, 1872.

temperature of the animal, and the loss from the apparatus by external cooling. By this method it was found, as the average result of five observations, that a dog of 5.392 kilogrammes' weight, at rest and in the fasting condition, produced in one hour 12.63 heat units; that is, 2.34 heat units for every kilogramme of bodily weight. According to these experiments, the heat-producing power in the dog and that in man are nearly the same; that of the dog being rather the more active of the two.

Normal Variation of Temperature in the Living Body.—The temperature of the body is not the same throughout, but increases, for a certain distance, from the exterior toward the central parts. Like any other substance of higher temperature than the air, the animal body is constantly losing heat from its surface; so that the integument and the parts immediately subjacent, which are more exposed to this cooling influence than the internal organs, have a temperature slightly below that of the body in general. Accordingly, whenever the external air rises to the neighborhood of 37° or 37.5° C., it feels uncomfortably warm; because, although this is the normal temperature of the internal organs, it is considerably above that of the skin, which is readily sensitive to variations of cold or warmth. The cooling influence of the atmosphere is, however, moderated by the circulatory movement of the blood; since the warmer blood coming from the internal parts supplies the integument with fresh quantities of heat, and thus tends to compensate for its external loss.

But notwithstanding this compensation, the difference in temperature between the external and internal parts of the body is always perceptible during health. If the bulb of a thermometer be held for some minutes between the folds of skin in the palm of the hand, it will stand at 36.4°; in the axilla, at 36.6°; under the tongue, it will reach 37.2°; in the rectum, 37.5°; and Dr. Beaumont found, in the case of Alexis St. Martin, that the thermometer, introduced into the stomach through the gastric fistula, often indicated a temperature of 37.8°. It is evident that, in order to ascertain the internal temperature of the body, the bulb of the thermometer should be inserted so deeply as to pass beyond the superficial zone affected by the process of external cooling. Even when beneath the tongue it is in contact with parts which are slightly cooled by the passage of the air in respiration, and accordingly does not reach the maximum temperature of the body. For this, it must be so deeply inserted into the abdominal cavity or the rectum, that a further introduction produces no increase in the indicated temperature. This is the method usually adopted in physiological observations.

Beside the difference from the above cause between the surface and the interior, the internal temperature also varies within narrow limits, according to different physiological conditions. Jürgensen * has shown

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* Die Körperwärme des gesunden Menschen. Leipzig, 1873.

that in man there is a *diurnal* variation, the temperature during the day being a little higher than at night, even when both periods are passed in complete repose. A series of observations on the same individual in a state of rest gave the following averages:

TEMPERATURE OF THE HUMAN BODY WHEN AT REST.

By day.	By night.
37.34°	36.91°

The difference between the two averages amounts to 0.43°. There are also temporary variations of small extent during each of the above periods; the greatest variation during the day being 0.27°; that during the night 0.15°.

The temperature of the body is also increased by *muscular activity.* It is a matter of common observation, both in man and animals, that temporary exertion produces an increase of bodily warmth. Jürgensen observed in the same individual that while during a day of absolute rest, the maximum temperature attained was 37.7°, under the influence of exercise it reached 38.8°. A much more striking difference, corresponding with muscular repose or activity, has already been mentioned as observable in insects.

The animal temperature is furthermore increased or diminished by a condition of *digestion or abstinence.* This was indicated in several instances by the observations of Jürgensen on man, but is shown in a marked degree by those of Senator on the dog, in which the production of heat was sensibly diminished by fasting, and increased by food. The following table shows the heat produced by the same animal under these two conditions:

QUANTITY OF HEAT PRODUCED BY THE DOG IN ONE HOUR.

After two days' fasting	10.90	heat units.
After one day's fasting	12.63	"
One hour after feeding	18.87	"

As the production of animal heat can only take place by the consumption or alteration of the bodily ingredients, it is evident that during abstinence from food, the materials susceptible of this change must diminish in quantity; and the temperature of the body after a time becomes lowered, owing to a deficiency in its sources of supply.

Mode of Production of Animal Heat.

In all instances, so far as observation goes, the production of heat in living organisms is in proportion to the activity of their internal changes. These changes are especially indicated by the absorption of oxygen and the exhalation of carbonic acid. Even in vegetables, it has been demonstrated that the absorption of oxygen is always accompanied by the exhalation of carbonic acid and the production of heat; and the quantity of heat produced is greatest during the processes of germination and flowering, which are accompanied by the most active absorption and exhalation of oxygen and carbonic acid respectively.

A similar relation is manifest in the animal kingdom. Birds and mammalians, whose respiration is most active, have the highest temperature; while in reptiles and fish, where the respiration is sluggish, the production of heat is also less abundant. The connection between the two phenomena is especially observable in hibernating animals, in which, during the winter sleep, respiration becomes comparatively inactive, and the bodily temperature is reduced to a very low standard. In the observations of Horvath* on marmots, he found that these animals during cold weather are plunged in a profound stupor, in which their respiration is very infrequent and sometimes hardly perceptible. At certain intervals they awake for a short time, and again return to the state of insensibility. The internal temperature of the animal, when awake, was from 35° to 37° C.; while, in the hibernating condition, it was reduced to 10°, 9°, or even to 2°, according to that of the surrounding air. On awaking, the temperature rapidly rises. In one animal, during sleep, it was from 9° to 10°; but on awaking it rose in one hour to 12°, in two hours to 17°, and in two hours and a half to 32°. Respiration varies in activity to a similar degree. A marmot weighing 153 grammes produced, while in the comatose condition, 0.015 gramme of carbonic acid per hour; and two days afterward, when awake, produced 0.513 gramme in the same time, that is, more than thirty times as much as when in the state of hibernation.

These facts indicate so close a relation between the intensity of respiration and that of heat production, that either one of these processes may be taken, in general terms, as the measure of the other; particularly as respiration consists in the absorption of oxygen and the exhalation of carbonic acid, and as the oxidation of carbonaceous matters, outside the body, is one of our readiest means for the production of heat.

But respiration is not exclusively connected with heat-production. It is essential to all the manifestations of animal life, and may be taken as the criterion of vital activity in general; and a further study of its phenomena shows that the heat of the living body cannot be considered as due to direct oxidation.

The Evolution of Heat and the Products of Respiration not strictly proportional. — Notwithstanding the general relation in activity between respiration and heat-production, a comparison of the quantity of heat produced, and that of oxygen absorbed or of carbonic acid exhaled, under different circumstances, shows that they do not exactly correspond with each other. In the observations of Senator on dogs, the evolution of heat and the production of carbonic acid did not follow the same rate of increase. They were both augmented during digestion, but the production of carbonic acid never increased to the same degree with that of heat. The averages obtained in three series of observations gave the following result:

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* Revue des Sciences Médicales. Paris, 1873, tome i., p. 59.

QUANTITIES OF HEAT AND OF CARBONIC ACID PRODUCED BY THE DOG IN ONE HOUR.

	Condition of the animal.	Carbonic acid in grammes.	Heat units.	Proportion between the two.
Dog No. 1	Fasting	3.455	12.630	1 to 3.65
	In digestion . . .	5.013	18.875	1 to 3.76
Dog No. 2	Fasting	4.405	16.500	1 to 3.72
	In digestion . . .	4.837	19.390	1 to 4.01
Dog No. 3	Fasting	3.154	16.880	1 to 5.35
	In digestion . . .	3.846	21.960	1 to 5.71

Thus the proportion of carbonic acid formed to the heat produced is different in the three animals when compared with each other in the same condition; and it also varies in each animal under the different conditions of fasting and digestion.

The same observer found that under the influence of a low temperature in a state of repose, the production of heat was never increased, but was usually diminished; while that of carbonic acid was generally somewhat increased and never diminished.

Local Production of Heat in the Organs and Tissues.—Although the body, as a whole, presents a general standard temperature, its heat is produced in each separate organ and tissue by the local acts of nutrition. This is shown by the fact that each organ has a special temperature of its own, which increases or diminishes according to its condition of activity or repose. A large quantity of heat is produced in the substance of the *muscles.* In the experiments of Becquerel and Breschet, the temperature of the brachialis muscle, in a man, during repose was 36.5°; but, after repeated and energetic flexion, it was from 37° to 37.5°. Bernard,* by placing thermo-electric needles in the gastrocnemii muscles of a dog, after section of the spinal cord to prevent voluntary movements, found the temperature of the muscles on the two sides sensibly equal; but on producing contraction by galvanizing one sciatic nerve, the temperature of the muscle on that side was increased 0.1° or 0.2°, while the venous blood returning from it became darker in hue. Since the muscles constitute so large a part of the mass of the body, it is evident that continuous muscular exertion must, after a time, produce a general elevation of temperature. In the muscles, during contraction, the increase in warmth is accompanied by greater consumption of oxygen, and consequently by a darker color of their venous blood.

Heat is also produced in the *glandular organs* when in active secretion, as shown by the temperature of the blood entering and leaving their tissue. Under these circumstances the venous blood coming from the gland is warmer than the arterial blood with which it is supplied. According to the observations of Bernard on the dog, while the submaxillary gland is in repose, its circulation is slow, and its venous blood scanty and dark-colored; the oxygen of the blood being reduced,

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* Revue Scientifique. Paris, 1871, No. 1, p. 1064.

while traversing the organ, to 40 per cent. of its original quantity. But when the gland is excited to active secretion, its circulation is increased in rapidity, and its venous blood more abundant and brighter in color; its oxygen being only reduced to 61 per cent. of that in arterial blood. At the same time the temperature of the gland rises, notwithstanding that its consumption of oxygen is less than in a condition of repose.

A similar elevation of temperature takes place in the blood while traversing the capillary circulation of the intestine and of the liver. The following tables give the results of two series of observations by Bernard on the temperature of the blood entering and leaving these organs in the dog:

Temperature of the Blood in the

Aorta.	Portal Vein.
36.8°	38.8°
40.3°	40.7°
39.4°	39.5°

Portal Vein.	Hepatic Vein.
40.2°	40.6°
40.6°	40.9°
40.7°	40.9°

Thus the blood of the hepatic vein, after traversing two successive capillary circulations, is warmer than that in any other part of the body.

Even in the kidneys, when the secretion of urine is active, there is a rise of temperature in the blood of the renal veins. At the same time, as in the submaxillary glands, the circulation is increased, the venous blood leaves the organ of a bright red color, and its proportion of oxygen, according to Bernard, is only reduced to 88 per cent. of that contained in the arteries, while in the condition of glandular repose it is reduced to 33 per cent.

It is evident, therefore, that animal heat may be derived from other causes than the immediate consumption of oxygen and formation of carbonic acid. Even outside the body heat may be produced by the hydration of quick-lime, or by the mixture of water with alcohol or sulphuric acid; and the changes of nutrition, consisting largely of hydrations, and other chemical or physical actions in which direct oxidation does not take part, are sufficient to account for the heat-production within the living frame. This heat-production is a local process, and takes place with different degrees of intensity according to special acts of nutrition in different organs. In the muscles it is accompanied by increased consumption of oxygen and deeper coloration of the venous blood; in the salivary glands and the kidneys by diminished consumption of oxygen and a less complete change in the color of the blood. The temperature of the blood coming from each organ is in proportion to the activity of heat-production in the organ itself; that of the venous blood consequently varies in different parts, while that of arterial blood is everywhere sensibly the same.

Cooling of the Blood in the Lungs and Skin.—While in the other internal organs the blood is warmed during its passage through the capillary vessels, in the lungs its temperature is slightly diminished. This fact, which has been alternately asserted and denied, owing to the difficulty of excluding incidental causes of error, has been abundantly confirmed by the observations of Hering, Bernard, Heidenhain and Körner, and Stricker and Albert. That of Hering was made on a young calf, otherwise in good condition, but having the malformation of ectopia cordis, so that the heart was unaffected by the contact of other organs. In this case the blood of the right ventricle had a temperature of 39.37°, that of the left ventricle 38.75°. Heidenhain and Körner,* in 94 observations on the dog, partly with thermo-electric needles and partly with the mercurial thermometer, found the temperature of the blood equal on the two sides of the heart in only one instance. In all the others, it was higher on the right side than on the left, by 0.1° to 0.6°. Bernard,† who first demonstrated this difference by the mercurial thermometer, has shown it also by the use of thermo-electric needles, introduced into the right and left ventricles of the dog's heart, through the jugular vein and carotid artery respectively; always finding the blood in the right ventricle warmer than that in the left. According to these observations, the difference in temperature may amount in the fasting animal to 0.174°, during digestion to 0.232°. Although during digestion the temperature of the blood generally is higher than in the fasting condition, the difference between the two sides of the heart continues to show itself in the same direction.

The diminution in temperature of the blood while passing through the lungs is usually attributed to the cooling influence of the air in the pulmonary cavities and to the vaporization of watery fluid. As the air expelled by respiration is warmer than when introduced into the lungs, it must withdraw a certain amount of heat from the internal parts; and as it contains watery vapor disengaged from the lungs, the vaporization of this fluid must also reduce the temperature of the organs. Whether these causes are more or less than sufficient to account for the difference in the blood on the two sides of the heart has not been determined. It is possible that a certain amount of heat is produced in the lungs, as in other internal organs; and that the heat so produced is more than counterbalanced by that lost from the pulmonary surface, the total effect on the blood being consequently a lowering of its temperature. In the cutaneous circulation similar causes exist for a cooling effect on the blood; namely, the contact of the air, and the vaporization of watery fluid supplied by perspiration. It is for this reason that the superficial parts of the body are less warm than the interior; and accordingly the blood, after passing through the vessels of the integument, returns to the centre with its temperature slightly diminished.

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* Archiv für die gesammte Physiologie. Bonn, 1871, Band iv., p. 558.

† Revue Scientifique. Paris, 1871, No. 1, p. 946.

The amount of warmth thus lost will vary with the degree of external cold and other conditions influencing the abstraction of heat.

Local Elevation of Temperature by Increased Circulation.—If the circulation be increased in any part of the integument, the effect produced is a local rise of temperature. This was shown by Bernard in his experiments on division of the sympathetic nerve. In the rabbit this operation produces a relaxation of the blood-vessels on the corresponding side of the head, an increased vascularity of the parts, most readily seen in the semi-transparent tissues of the ear, and a higher temperature, perceptible both by the touch and by the thermometer. After section of the sympathetic nerve on the right side, the temperature of the corresponding ear was increased from 25° to 32° C.; the difference between the two sides being usually more marked in a cold atmosphere. As the superficial parts of the body are habitually cooler than the internal, from their exposure to the air, and as they are constantly supplied with warm blood from the interior, their temperature will be raised by an increase in the amount of blood circulating through them. The rise of temperature in these cases is a passive one, the exposed tissues being warmed at the expense of the blood coming from the interior. No more heat is produced than usual, and the cooling effect of the air on the surface is unchanged; but it is less perceptible in the part subjected to experiment, owing to its increased supply of blood, and the larger quantity of heat brought to it in a given time.

The influence of the circulation upon the temperature of the external parts has been shown by Mitchell* in observations on the human subject. If the hand and arm be held for some moments above the head, emptied as fully as possible of blood, and a tourniquet then applied to the arm in such a way as to check the circulation, the temperature of the hand falls 0.55°. If on the contrary, the circulation be left unimpeded, and a freezing mixture applied to the elbow, sufficient to chill the ulnar nerve, when sensation has become entirely abolished the temperature of the corresponding hand rises 1.10° or even 2.20°. But if the arm be emptied of blood, the tourniquet applied, and the ulnar nerve then chilled to insensibility, the temperature of the hand no longer rises, but falls, as before, 0.55°. This shows that the rise of temperature, in the second experiment, was due to increased circulation of blood in the paralyzed parts.

In the glandular organs, on the other hand, when in functional activity, the rise of temperature is an active one, taking place in the substance of the gland itself; since the blood passing through these organs becomes warmer instead of cooler, and receives heat from changes taking place in the glandular tissue.

Equalization of Bodily Temperature by the Circulation.—As the production of heat varies in different parts, according to their nutritive changes, the blood acquires a higher temperature in some organs than

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* Archives of Scientific and Practical Medicine. New York, 1873, vol. i., p. 354.

in others; while in the lungs and skin its heat diminishes instead of increasing. If the blood remained at rest, these differences would be still more marked. But as it is in constant motion, from the circumference to the centre, and again from the centre to the circumference, the effect of the circulation is to equalize, in great measure, the temperature of different parts. The blood coming from the general integument with a diminished temperature is mingled with that of the muscular system, which has become warmed during its capillary circulation. The blood of the hepatic veins, which is the warmest of all, joins the current of the inferior vena cava, with a somewhat lower temperature, returning from the pelvic organs and the inferior extremities. It is again mingled, at its entrance into the right cavities of the heart, with the blood descending from the head and upper extremities by the superior vena cava. The whole volume of the blood then passes through the lungs, with the effect of still further moderating its temperature; and the arterial blood is distributed to the various parts of the body, to gain warmth in some and to lose it in others, and to be again mingled after a few seconds at the centre of the circulation. The superabundant heat of certain organs, where its production is most active, is constantly transferred to others by the moving column of the blood; and a certain equilibrium of temperature is thus established for the body as a whole. In the observations of Jürgensen, this standard temperature, as measured in the rectum, was found to vary, within narrow limits, from day to night, and even at successive periods in the twenty-four hours. These fluctuations are no doubt due to the varying functional activity of different parts; the total amount of heat produced being increased or diminished with the preponderating influence of organs in which it is more or less rapidly generated.

Regulation of the Animal Temperature.

A certain temperature is not only the result of the vital actions; it is also necessary to their accomplishment. Even in vegetables this temperature, which varies within moderate limits in different plants, is requisite for all the phenomena of growth and vitality. A seed sown in the most productive soil does not germinate except under the influence of the necessary warmth; and its germination is also impossible if it be exposed to a heat which is too intense. The degrees both of heat and cold which favor or arrest the functions of vegetation have been in many instances accurately determined. According to Sachs, the limits of germination for wheat and barley are between 5° and 38° C., and for Indian corn between 9° and 42°. The irritability and periodic movements of the sensitive-plant do not show themselves unless the temperature of the surrounding air be above 15°. In air at 48° to 50°, on the other hand, the leaflets become rigid in a few moments, though they may afterward recover if the temperature be moderated; while a heat of 52° permanently destroys their vitality. Thus no vegetative function can come into activity, unless the temperature of the plant reaches a certain degree above freezing; and it ceases at another determinate temperature, which cannot for any considerable time exceed 50°. Within these two limits every vegetable function has a special temperature at which it is most active; diminishing in intensity both above and below this point.

The same is true of the animal functions. Each species of animal has a definite bodily temperature, which cannot be raised or lowered beyond certain limits without injury. Mammalians, whose normal temperature is from 37° to 40°, become insensible and soon die, when cooled down to 18° or 20°, which is the natural standard for reptiles and fish; while a frog is killed by being kept in water at 38°. On the other hand, mammalians die when their blood and internal organs are heated up to 45°, which is precisely the normal temperature of birds; and birds are fatally affected when their temperature is raised to 48° or 50°. In every case the vital functions are seriously disturbed by a very moderate change in the temperature of the bodily organs; and in the mammalians, as a rule, death follows when this change amounts to an elevation of 6° or 7°, or to a depression of 20°.

In man, in febrile affections, the rise of temperature, as measured in the axilla, yields a very accurate criterion of the gravity of the disease. An increase of this temperature from 36.6° to 37.5° or 38° C. indicates a mild form of the malady; but an increase to 40° or 40.5° shows that the attack is severe. Above 40.5° it is a symptom of great danger; and when it rises to 42.5° or 43° a fatal result is almost inevitable.*

Effects of Lowering the Temperature of the Animal Body.—If a warm-blooded animal or man be exposed to cold in such a way that the internal heat is abstracted faster than it can be produced, the effect is a general depression of the vital functions. After a short period of pain in the more exposed parts, the skin becomes insensible, the muscles lose their energy, the movements of respiration diminish in frequency, and the nervous system becomes inactive. In man a marked sluggishness of mind, and a disposition to sleep have been observed as among the symptoms of continued exposure to unusually low temperatures.

The general effects of a low temperature result from its combined influence on all the organs and tissues. According to Bernard, if a rabbit or guinea-pig be subjected to continuous abstraction of heat, the temperature of the animal, as taken in the rectum, gradually falls from 38° to 30°, 25°, 20°, and 18°. When the depression has reached this point, there is general insensibility and paralysis, with feeble and infrequent respiration. The heat-producing power is also lost, so that if the animal be withdrawn from the apparatus, and kept in the air at 10° or 12°, its temperature, nevertheless, continues to diminish, and death takes place after a short time.

But when in this condition, although most of the vital actions are suspended, and the animal has lost the power of maintaining his own

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* Flint, Principles and Practice of Medicine. Philadelphia, 1868, p. 109.

temperature, if he be supplied with artificial warmth up to a certain point, he may regain his vitality, and the processes of life be again put in operation. The respiration, which had been reduced to a minimum by the action of cold, gains in rapidity as the body is artificially warmed, and the functions of the nervous and muscular systems are finally restored.

A striking example of temporary suspension of the bodily functions by cold is presented by the *hibernating animals*, which pass into a condition of torpor during the winter, becoming insensible, unconscious, and motionless, while respiration is nearly imperceptible, and the bodily temperature sinks to 10°, or even below it. Life, however, is not abolished, but only held in abeyance; and with the return of spring all the functions resume their activity. A hibernating animal is somewhat in the condition of a seed, which remains in the ground over winter, with its vitality dormant, and ready to come into action when supplied with the requisite warmth.

Effects of Elevating the Temperature of the Animal Body.—If the temperature of the body be raised above the normal standard, the effects are quite different from those produced by cold. In the observations of Bernard, on birds and mammalians confined in heated air, with due ventilation, the primary effects were increased frequency of respiration with discomfort and agitation; and death was usually accompanied with convulsive movements, or preceded by an audible cry. The fatal result was more rapidly produced in birds than in mammalia. A rabbit, in air at 65°, died in twenty minutes; and a bird, in air at the same temperature, in four minutes. This difference is probably due to the greater activity of the circulation in birds, by which external heat is more rapidly transferred to the internal organs; since the same observer found that when two rabbits, one living and one dead, were placed in air at 100°, the internal temperature of the living animal became sensibly raised sooner than that of the dead one. In a medium of high temperature, therefore, a fatal amount of heat reaches the internal organs more rapidly by the circulation than by conduction through the solid tissues.

After death from exposure to too warm an atmosphere, the internal temperature is found to be 5° or 6° above the normal standard; the heart is motionless; both the muscles and the nerves are insensible to galvanism; and cadaveric rigidity is established with unusual promptitude. In many instances the blood is found dark-colored in the arterial as well as in the venous system; but this is a post-mortem change, since observation shows that the arterial blood continues red during life, while its oxygen disappears and its color darkens after the stoppage of respiration. A high temperature produces death apparently by hastening, in undue measure, the chemical changes in the tissues and fluids, so that their vitality is rapidly exhausted and can no longer be maintained by the usual processes of nutrition.

Resistance of the Body to Low External Temperatures.—Since an actual depression of the temperature of the body is followed by such serious results, and since its warmth is maintained during health at the normal standard, notwithstanding exposure to varying degrees of cold, it is evident that the living organism possesses the power of increasing its internal production of heat, to compensate for greater loss without. It is a matter of common observation, that moderate external cold, if not too long continued, produces a sense of warmth and increased vigor, instead of depression. The atmosphere of a winter's day, or a cold shower-bath, acts as a stimulant to the vital processes; and although the exposed parts of the skin may be reduced below their normal temperature, the body, as a whole, does not experience a loss of warmth, but maintains its natural condition of vitality. It is certain that in these circumstances more heat must be produced under the influence of external cold.

The mode in which this result is accomplished has not been determined with precision. It is plain that the nervous system has its share in the process, perhaps by directly stimulating the molecular changes which are active in heat-production. There are, however, two sources of heat-supply, which evidently play an important part in maintaining the temperature of the body under exposure to cold.

The first of these is *muscular activity*. It has been shown that the muscles produce a considerable quantity of heat in their own tissue, and that this quantity is increased by muscular contraction. The total production of heat, therefore, for the whole body, must be augmented when the voluntary muscles are thrown into activity. Experience shows that this is, in fact, one of the requisite conditions of resistance to cold. The stimulus of cool air upon the skin excites the desire for active movement, and muscular exercise produces a compensating quantity of internal heat. But if the body be exposed to even moderate winter weather without voluntary motion, it must either be protected by an unusual quantity of clothing, or it will soon feel a depressing effect from the loss of its animal heat.

Secondly, an increased production of warmth is provided for by *increased supply of food*. The requisite materials for heat-production, in the substance of the tissues, are primarily derived from the ingredients of the food. Even a recent ingestion of food, as shown by Senator, increases perceptibly, in the dog, the amount of heat generated within a given time; and for longer periods, the influence of an ample or a scanty supply is abundantly manifest. In animals which are insufficiently fed or ill-nourished, the capacity for resistance to cold is much less than in those which are in good condition and which have received a fair quantity of food. The effect of moderate exposure to cold in the healthy condition, is to increase the appetite. A larger quantity of food is habitually taken during the winter than in summer; and among the inhabitants of northern and arctic regions, the daily consumption is greater than in temperate and tropical climates.

It is not necessary to assume that the food, thus required for heat-production, furnishes directly the necessary warmth by its consumption. The heat is no doubt generated from the nutritive changes in the bodily tissues, and these changes are continued only by a supply of food sufficient to provide for the demands of the system.

Resistance of the Living Body to High External Temperatures.—It has been seen that, in man and warm-blooded animals generally, a rise in the bodily temperature of 6° or 7° is certainly fatal; and yet the body may be exposed, as shown by repeated observations, to much higher degrees of heat without injurious result. According to Carpenter,* the temperature of the air, in many parts of the tropical zone, rises daily, through a large portion of the year, to 43° C. In southern Arizona, the temperature at midsummer, as observed by Pumpelly,† ranges, in the shade, from 47° to 52°; and it is well known that the air of manufactory drying-rooms and of the Turkish bath may easily be endured when considerably above 45°. Either of these temperatures would be fatal to man, if they indicated the actual warmth of the internal organs. The body therefore must either possess some means of diminishing its own heat-production, or else of compensating, to a certain extent, external temperatures which are above the normal standard.

The most direct means of moderating the temperature of the body is the *cutaneous perspiration*. This secretion, derived from the perspiratory glands of the skin, is clear, colorless, and watery, with an acid reaction, and a specific gravity of 1003 or 1004.

It is a fluid of very simple composition, containing over 99½ per cent. of water, and more than half its solid ingredients consisting of inorganic salts. There are also traces of an organic substance similar to albumen, and a free volatile acid, which gives to the secretion its reaction and odor.

The perspiration is a continuous secretion. In a condition of repose or moderate bodily activity, it is exuded so gradually that it is at once carried off by evaporation, and has received the name, under these circumstances, of the *insensible transpiration*. The quantity of fluid discharged in this way, according to Lavoisier and Seguin, amounts on the average to 900 grammes per day. In addition to this, about 500 grammes are discharged from the lungs, making 1400 grammes of daily exhalation from the whole body. The vaporization of this quantity of water will consume 750 heat units; or about one-fifth of all the heat produced in the body during twenty-four hours.

The cutaneous perspiration may be increased by temporary causes. An elevated external temperature or unusual muscular exertion, will accelerate the circulation through the skin, and largely augment the amount of fluid discharged. It may then exude more rapidly than

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* Principles of Human Physiology. London, 1869, p. 483.

† Across America and Asia. New York, 1871, pp. 41, 57, 59.

it can be carried off by evaporation, collecting upon the skin as a visible moisture, when it is known as the *sensible* perspiration. The amount discharged during violent exercise has been known to rise as high as 380 grammes per hour; and Southwood Smith* found that laborers in heated gas-works sometimes lost, by both cutaneous and pulmonary exhalation, nearly 1600 grammes in the same time. The evaporation of this increased quantity of fluid neutralizes the effect of the heated atmosphere, and thus prevents an undue rise of the bodily temperature.

It is possible that certain influences transmitted through the nerves may also have the power of controlling directly the molecular activity of the tissues, and may thus diminish the amount of internal heat at the source of its production; but the experimental evidence of this action is yet incomplete, and its mode of operation comparatively obscure.

The production of animal heat, and the regulation of the bodily temperature, by which it is maintained at or near a normal standard, are two of the most important phenomena presented by the living organism. They result from an associated series of vital actions, and are at the same time essential conditions for the continuance of life.

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* Philosophy of Health. London, 1838, chap. xiii.

CHAPTER VI.

THE CIRCULATION.

THE circulatory system is an apparatus by which the blood is transported to different regions of the body, and by which, after serving for nutrition, absorption, or secretion, it is returned to the lungs for aeration. By this movement of the blood in a continuous circuit, the materials absorbed in the alimentary canal are conveyed to distant parts for their nourishment and growth, the oxygen taken in by the lungs is distributed throughout the body, the products of excretion find their way to the outlets of the system, and the losses by exhalation in one organ are made good by absorption in another. The mechanical function by which this is accomplished is regulated by the conditions of compression, fluidity, and resistance, under which the blood moves through the blood-vessels.

The circulatory apparatus consists of four different parts, namely, 1st. The heart, a hollow, muscular organ, which propels the blood. 2d. The arteries, a series of branching tubes, which convey it to different parts of the body. 3d. The capillaries, a network of inosculating tubules, interwoven with the substance of the tissues, bringing the blood into intimate relation with their component parts; and 4th. The veins, a system of converging vessels, which collect the blood from the capillaries, and return it to the heart. In each of these different parts of the circulatory apparatus, the movement of the blood is dependent on special conditions.

The Heart.

The structure of the heart and its relation with the adjacent vessels, is particularly connected with the activity and mechanism of respiration. In man and mammalians, this function is very active, and is performed almost exclusively by the lungs. The whole of the blood, accordingly, after returning from the periphery, passes through the lungs before it is again distributed to the system at large. It thus traverses in succession the general circulation for the whole body, and the special circulation of the lungs. The mammalian heart (Fig. 57), consists of a right auricle and ventricle (*a*, *b*), receiving the blood from the vena cava (*i*), and driving it to the lungs; and a left auricle and ventricle (*f*, *g*) receiving the blood from the lungs and propelling it outward through the arterial system.

It is, therefore, a double organ, with two sets of muscular cavities, right and left; its right cavities being devoted to the circulation through the lungs, its left cavities to that through the general system. It is of a somewhat conical form; its base, situated upon the median line, being directed upward and backward, while its apex, in man, points downward, forward, and to the left, surrounded by the pericardium, but capable of a certain degree of lateral and rotatory motion. The auricles, which have a smaller capacity and thinner walls than the ventricles, are situated at its upper and posterior part, while the ventricles occupy its anterior and lower portions. The two ventricles, moreover, are upon different planes. The right ventricle is somewhat in front and above the left; so that in an anterior view the greater portion of the left ventricle is concealed by the right, and in a posterior view the greater portion of the right ventricle is concealed by the left; while in both positions the apex of the heart is constituted altogether by the point of the left ventricle.

Fig. 57.

Diagram of the Heart and Pulmonary Circulation in Mammalians.—*a.* Right auricle. *b.* Right ventricle. *c.* Pulmonary artery. *d.* Lungs. *e.* Pulmonary vein. *f.* Left auricle. *g.* Left ventricle. *h.* Aorta. *i.* Vena cava.

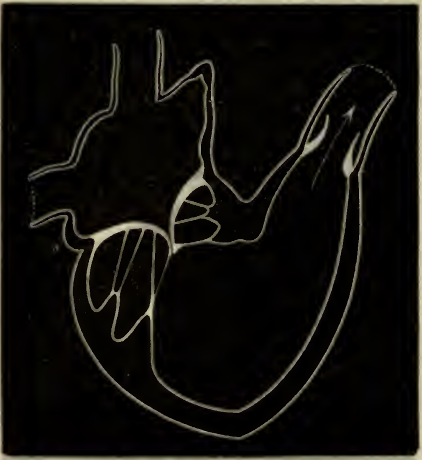
Fig. 58.

Right Cavities of the Heart; Auriculo-ventricular Valves open, Arterial Valves closed.

The cavities of the heart and of the adjacent blood-vessels on each side, though continuous with each other, are partially separated by certain constructions. The orifices by which they communicate are known by the names of the auricular, auriculo-ventricular, and aortic and pulmonary orifices; the auricular orifices being the passages from the venæ cavæ and pulmonary veins into the right and left auricles; the auriculo-ventricular orifices leading from the auricles into the ventricles; and the aortic and pulmonary orifices leading from the ventricles into the aorta and pulmonary artery respectively.

The auriculo-ventricular, aortic, and pulmonary orifices are fur-

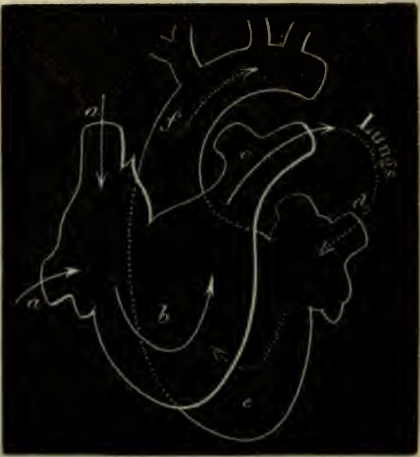
Fig. 59.



Right Cavities of the Heart; Auriculo-ventricular Valves closed, Arterial Valves open.

nished with valves, which allow the blood to pass from the auricles to the ventricles, and from the ventricles to the arteries, but close against its return in the opposite direction. The course of the blood through the heart is, therefore, as follows. From the vena cava it passes into the right auricle; and from the right auricle into the right ventricle. On the contraction of the right ventricle, the tricuspid valves shut back, preventing its return into the auricle (Fig. 59); and it is driven through the pulmonary artery to the lungs. Returning from the lungs, it enters the left auricle, thence passes into the left ventricle, from which it is delivered into the aorta, and distributed throughout the body. The two streams of blood, arterial and venous, in their passage through the heart, follow, in each case, a curvilinear and more or less spiral direction; the axes of the currents crossing each other in the right and left cavities respectively (Fig. 60). The venous blood, received by the right auricle from the venæ cavæ, passes downward and forward into the ventricle. It there turns from below upward, from right to left and from before backward, through the conus arteriosus, to the pulmonary artery. On returning from the lungs to the left auricle, it passes downward into the left ventricle, when it makes a turn like that upon the right side, passing from below upward and from left to right, behind the conus arteriosus, and crossing its axis at an acute angle, to the commencement of the aorta. The aorta, though at its origin somewhat posterior to the pulmonary artery; soon comes to the front in its arched portion, while the pulmonary artery runs almost directly backward. Thus the two blood-currents twist spirally round each other in their course.

Fig. 60.



Course of Blood through the Heart.—a, a. Vena cava, superior and inferior. b. Right ventricle. c. Pulmonary artery. d. Pulmonary vein. e. Left ventricle. f. Aorta.

The passage of the blood through the heart is accomplished by alternate contraction and relaxation of its muscular walls; by which successive portions are delivered from the auricles into the ventricles, and thence into the arteries. Each movement of this kind is called a beat or *pulsation* of the heart. The cardiac pulsations are accompanied by certain phenomena dependent on the structure of the organ and its mode of action.

Sounds, Movements, and Impulse of the Heart.—The sounds of the heart are two in number, differing from each other in time, tone, and duration. They are known as the *first* and *second* sounds, and may be heard on applying the ear to the chest at the cardiac region. The first sound is loudest over the anterior surface of the heart, particularly at the situation of the apex beat, over the fifth rib and fifth intercostal space. It is comparatively long and dull in tone, and occupies one-half the duration of a beat. It corresponds in time with the impulse of the heart in the precordial region, and with the stroke of the large arteries in the vicinity of the chest. The second sound follows almost immediately upon the first. It is most audible at the situation of the aortic and pulmonary valves, namely, over the sternum at the level of the third costal cartilage. It is short and distinct, and occupies about one-quarter of the time of a pulsation. It is followed by an equal interval of silence; after which the first sound recurs. The whole time of a pulsation may be divided into four quarters, of which the first two are occupied by the first sound, the third by the second sound, and the fourth by an interval of silence, as follows:

Time and Duration of the Heart-Sounds.

Cardiac pulsation	1st quarter 2d "	First sound.
	3d "	Second sound.
	4th "	Interval of silence.

The *first* sound of the heart is mainly produced by the tension and consequent vibration of the auriculo-ventricular valves and chordæ tendineæ at the time of ventricular systole. It may be imitated by alternately loosening and extending a tape or ribbon, with its ends firmly held between the fingers of the two hands. According to Chauveau and Faivre,* when the tension of the auriculo-ventricular valves is prevented, in the horse, either by dividing the chordæ tendineæ, or by inserting into the auriculo-ventricular orifice a short tube, from 1½ to 2 centimetres in diameter, the sound is changed in character, and replaced by a soft murmur; a reflux of blood, at the same time, taking place into the auricle. Valvular tension is therefore generally admitted, as a cause for the first sound, and by many observers is regarded as fully sufficient to account for it. There is a difference of opinion as to

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* Dictionnaire Encyclopédique des Sciences Médicales. Paris, 1876, tome xviii., p. 344.

the admixture of another element in its production, namely, the muscular contraction of the ventricular walls. But from the evidence thus far presented, it appears that the direct share of muscular contraction in the first sound, if it exist at all, must be secondary in importance to that of valvular tension.

The cause of the *second* sound is universally acknowledged to be the sudden closure and tension of the aortic and pulmonary valves, under the reaction of arterial pressure at the end of the ventricular systole. These valves are fibrous, semilunar festoons, which yield to the current of blood passing from the ventricle into the artery (Fig. 59), and which shut together in the form of distended sacs (Fig. 58) when the artery reacts upon its contents. Their connection with the second sound of the heart, which occurs at the same time, is established by the following proofs: 1st. The sound is heard with complete distinctness directly over the situation of these valves at the base of the heart; 2d. The farther we recede in any direction from this point, the fainter it becomes; and 3d. All experimenters agree that when the semilunar valves are hooked back against the inner surface of the artery by curved needles, or held open by fine springs introduced into the vessel, the second sound disappears, and remains absent until the valves are again liberated.

The difference in character between the first and second sounds of the heart is apparently due to the difference in size and attachment of the auriculo-ventricular and the semilunar valves. The former are comparatively broad sheets attached by their external edges to the auriculo-ventricular fibrous zones, and by their internal edges and lower surfaces, through the chordæ tendineæ, to the musculi papillares of the ventricular walls. The latter are of smaller size, and attached only to the fibrous zones at the base of the large arteries. In imitating the effect of valvular tension with a piece of ribbon or other woven fabric, a longer piece will yield a sound similar to the first sound of the heart, a shorter piece one similar to the second sound.

The *movements* of the heart may be observed in the dog, or other warm-blooded quadruped, after opening the chest by a longitudinal incision through the sternum and separating the costal cartilages on each side at their junction with the ribs; artificial respiration being maintained by the nozzle of a bellows inserted into the trachea. The animal may be etherized and rendered permanently insensible by trephining the skull, and applying cerebral compression, or he may be partially narcotized by a preliminary subcutaneous injection of morphine, after which etherization is produced, and continued with great facility. The operation of opening the chest and exposing the thoracic organs increases the rapidity of the heart's movements, and diminishes their force; but they often have sufficient vigor to continue with regularity for one or two hours, if artificial respiration be properly maintained.

When exposed to view by this means, the action of the heart is so complicated that it requires a close examination to appreciate its character. It is obvious at the outset that the organ presents itself in two different conditions, alternating with each other in rapid succession; namely, a condition of rest and a condition of movement. One of these is the condition in which it expels the blood from the ventricles into the arteries; the other is that in which the ventricles are again filled with blood from behind. The first object of the observer is to determine the time at which each one of these two conditions presents itself, and the physical changes in the organ by which it is accompanied. If the heart be touched or gently grasped by the fingers, its alternations of rest and movement are felt to correspond with similar variations in its consistency. At the time of rest it is comparatively soft and yielding; at the time of its movement it becomes hard and tense. If a slender silver canula be inserted, through the walls of the left ventricle, into its cavity, the blood is ejected from the outer extremity of the canula at the instant of the heart's tension and movement, while its flow is suspended in the intervals of repose.

It is evident, therefore, that the time of the heart's movement is that of the ventricular systole, in which the muscular walls of the ventricles close upon their contents, and propel the blood into the arterial system. Like other muscles, the heart assumes, at the instant of contraction, a condition of rigidity, readily perceptible on placing the fingers in contact with its surface.

If the muscular fibres of the heart ran in a straight direction between their points of origin and insertion, its changes of form and position, like those of most voluntary muscles, would be comparatively simple. But they are in the form of elongated curvilinear loops, which have their origin in the fibrous zones at the base of the organ, and, after embracing the ventricular cavities, return to be inserted into the same fibrous zones or into the chordæ tendineæ. As the entire heart, furthermore, is attached at its base, while its body and apex are movable, the united action of its fibres produces a combination of simultaneous movements different from those of other muscular organs.

In an anterior view of the dog's heart, the base of the organ, at each ventricular systole, appears to approach its apex. The point of the heart is at the same time protruded, tilted slightly from left to right, and rotated in the same direction on its longitudinal axis. The protrusion of the apex can be felt somewhat forcibly by the end of the finger applied lightly to its surface, and it can also be shown by the movement of a long steel needle suspended vertically on a horizontal axis, so that its lower extremity touches the point of the heart. At each cardiac systole, the upper end of the needle moves backward, as its lower end is thrown forward by the protrusion of the apex. At the same time, the body of the organ is increased in thickness from its anterior to its posterior surface, and diminished in its transverse diameter, that is, from the right to the left lateral border. All these phenomena depend on the anatomical arrangement of the contracting fibres.

The descent of the base of the heart in front toward its apex is due to the contraction of the right ventricle, which occupies most of the anterior surface of the organ, being wrapped round the left ventricle from below upward and from right to left, and continuing its course in this direction, as the conus arteriosus, to the base of the pulmonary artery. Its superficial muscular fibres run obliquely from above downward and from right to left, uniting with those of the left ventricle at the interventricular sulcus. The base of the heart in an anterior view is therefore the upper border of the right ventricle and conus arteriosus; and it is brought downward, by the contraction of the descending muscular fibres, toward the interventricular sulcus and the point of the heart. The principal part of the cardiac mass, in warm-blooded quadrupeds, consists of the left ventricle; while the right ventricle is an additional chamber or covered passage-way, leading to the pulmonary artery, very visible in a front view, owing to its situation, but forming a small portion of the substance of the organ. The relative volume of the two ventricles may be shown by a transverse section of the heart in its contracted condition. The left ventricle forms a thick muscular cone, with its cavity nearly in the centre of the cardiac mass; while the right ventricle is a comparatively inconsiderable layer of fibres attached to the surface of the organ and enclosing a cavity of more linear and flattened form. Its contraction, accordingly, may produce a marked change in the superficial aspect of the heart, without causing an important alteration in its entire form.

Fig. 61.

Transverse Section of the Bullock's Heart in the State of Cadaveric Rigidity.—*a*. Cavity of the Left Ventricle. *b*. Cavity of the Right Ventricle.

The deviation of the heart's apex toward the right, and its axial rotation in the same direction, at the ventricular systole, are caused by the obliquity of the external cardiac fibres, and the mode of their penetration at the apex. The most superficial of these fibres, running obliquely from above downward and from right to left, at the time of their contraction tilt the point of the heart slightly toward the right. Near the apex of the organ they curl round its axis, and suddenly change their direction, passing into the interior of the ventricles as deep-seated fibres, and thence running upward, to terminate in the chordæ tendineæ and auriculo-ventricular zones.

They thus form, exactly at the point of the heart, a whorl or vortex of converging fibres. Muscular fibres, arranged in this way, necessarily tend, in contracting, to straighten themselves and untwist the spiral. At the ventricular systole, therefore, the heart rotates on its axis, from left to right anteriorly, and from right to left posteriorly. This produces the twisting movement perceptible at the apex.

The protrusion of the point of the heart in contraction has been variously regarded; first as an elongation of the cone formed by the left ventricle, and secondly, as a movement of the whole heart, due to a recoil from the blood expelled from it under pressure, or to a reaction of the distended arteries at its base. Many of the earlier observers (Galen, Vesalius, Harvey, Riolanus, Borelli, Winslow) found the longitudinal diameter of the heart increased at the moment of systole, and its transverse diameter diminished. Pennock and Moore,* in 1839, in a series of experiments on sheep, calves, and horses, also observed an elongation, the extent of which they measured with a graduated rule. On the other hand some of the earlier, and nearly all the more recent writers of eminence (Lower, Haller, Longet, Carpenter, Flint, Ranke, Chauveau, Burdon-Sanderson) are of opinion that the heart shortens during systole, being diminished in both its longitudinal and transverse diameters. In our own observations we have always seen reason to admit that the forward movement of the apex is due to an elongation of the heart at the moment of systole. This is not easily perceptible in a front view, owing to the prominent action of the right ventricle on the anterior surface of the organ. But if the heart be tilted upward and viewed from its posterior surface, formed mainly by the left ventricle, while its base is firmly held by the fingers placed upon the great vessels, at every contraction its sides will be seen to approximate each other, and its point to protrude; that is, its longitudinal diameter is increased, and its transverse diameter diminished. The end of the finger in contact with the apex is forcibly thrown upward by the contracting ventricle, and a light rider of paper placed on the

Fig. 62.

Bullock's Heart, anterior view, showing the superficial muscular fibres.

Fig. 63.

Converging Spiral Fibres at the Apex of the Heart.—The direction of the arrows indicates that of the rotating movement of the heart at the ventricular systole.

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* Medical Examiner. Philadelphia, 1839, No. 44.

point of the heart is carried in the same direction. If an ivory or porcelain rod be held horizontally just above the heart in this position, the apex rises visibly toward the rod at each ventricular systole, and recedes from it in the same degree at each diastole.

Such an elongation can only be explained by the arrangement of the fibres in the ventricular wall. Every muscular fibre, during contraction, increases in thickness while diminishing in length; so that its volume remains the same. The superficial cardiac fibres which run obliquely downward to the point of the heart, and then turn upward along its internal surface to their insertion in the auriculo-ventricular zones, would have the effect, if they acted alone, to draw the point and base of the organ together and thus to shorten the heart. But between their superficial and internal layers there are deep-seated fibres, running in a nearly circular direction round the axis of the ventricular cavity. These circular fibres, which are nearly wanting on the right side, are very abundant in the left ventricle and form a large part of its muscular walls. In the ventricular systole they contract upon the blood in the ventricular cavity like the fingers of a closed hand. By their contraction they tend to obliterate the ventricular cavity, and by their lateral swelling at the same time they exert a pressure from the base of the heart toward its point, causing a protrusion of the apex.

Fig. 64.

Left Ventricle of Bullock's Heart, showing its deep fibres.

The *impulse* of the heart is a stroke of the apex against the walls of the chest, usually perceptible both to sight and touch, at the time of ventricular systole. In man it is felt, as a rule, in the fifth intercostal space, about midway between the left edge of the sternum and a vertical line drawn through the left nipple. But its location varies somewhat with the attitude and the respiration, owing to changes of position of the heart within the chest. In the recumbent posture, when lying on the left side, the situation of the heart's impulse is shifted from one and a half to two centimetres farther outward from the median line. When lying on the right side, it may be altogether imperceptible. In every posture it disappears when the chest is fully expanded in inspiration, as the cardiac surface is then completely covered by the lungs. But if inspiration be performed by the diaphragm alone, the chest remaining fixed, the descent of the heart, as it follows the diaphragm, is indicated by the changed position of the impulse. This is most distinctly shown in the recumbent posture on the left side; when, in moderate expiration, the heart's impulse is felt in the fifth intercostal space, but in full inspiration, using the diaphragm alone, it disappears from that point and is felt in the sixth intercostal space. In the erect posture the impulse may also be felt in the sixth intercostal space after full inspiration by the diaphragm alone.

The immediate cause of the cardiac impulse is, without question, the shock of the heart against the walls of the chest. Its character, its coincidence in time with the ventricular systole, its position, and its variation with the changes of attitude and respiration, all indicate its dependence on the muscular action of the heart's apex. As to the exact manner in which it is produced there is a difference of opinion. By some a large share is attributed to the direct protrusion of the apex and its lateral movement toward the right; both of which would bring it in contact with the chest with sufficient force to lift the integuments at the intercostal spaces. Others regard it as due to the sudden hardening of the ventricle at the time of systole and the slight increase in its antero-posterior thickness at the same time. It is certain that the heart in contraction acquires a much firmer consistency, and this undoubtedly adds to the effect of the protrusion and movement of the apex, as felt externally.

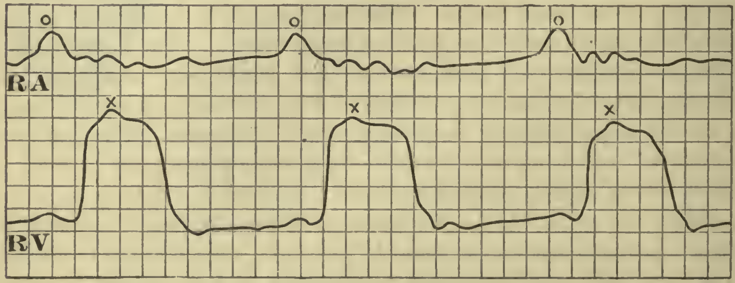
Rhythm of the Heart's Action.—The succession of phenomena in a cardiac pulsation consists of a double series of contractions and relaxations; namely, those of the auricles and those of the ventricles. The two auricles contract simultaneously with each other, and afterward the two ventricles; and in each case the contraction is followed by a relaxation. The auricular contraction, which is short and comparatively feeble, occupies the first part of the time of a pulsation. The ventricular contraction is longer and more powerful, and occupies the latter part of the same period. Then comes a short interval of repose, after which the auricular contraction again recurs. The auricular and ventricular contractions, however, are not completely separated from each other, like the alternate strokes of two pistons in a forcing-pump, but are in some measure connected and continuous. The muscular action, after beginning at the auricle, is at once propagated to the ventricle and runs rapidly toward the apex. The entire ventricle contracts vigorously, its walls harden, its point protrudes, impinges against the walls of the chest and twists from left to right, the auriculo-ventricular valves shut back, the first sound is produced, and the blood is driven into the arterial system. These phenomena occupy about one-half the time of pulsation. Then the ventricle is relaxed, and a period of repose ensues. During this period the blood flows from the large veins into the auricle, and through the auriculo-ventricular orifice into the ventricle; filling the ventricle, by a kind of passive dilatation, about two-thirds or three-quarters full. Then the auricle contracts with a quick motion, forcing the last drop of blood into the ventricle, and distending it to its full capacity; when the ventricular contraction again takes place, driving the blood into the large arteries. These movements alternate with each other, and form, by their recurrence, the successive cardiac pulsations.

The successive elements in a cardiac pulsation, and the corresponding variations of pressure in the auricular and ventricular cavities, are most distinctly shown by means of the double *cardiograph*, a registering apparatus, first employed by Marey.* The apparatus is composed of two parts; first, an instrument introduced into the cardiac cavities, to receive and transmit their variations of pressure; and secondly, a registering machine, by which these variations are permanently recorded.

The first instrument consists of two slender parallel tubes, of such length that, when introduced into the jugular vein of the horse, one will reach the cavity of the right auricle, the other that of the right ventricle. The lower extremity of each tube is widely fenestrated and covered with an elastic membrane, to receive the pressure of the blood in the cardiac cavity. The upper extremity is connected by a flexible tube with a shallow metallic cup or drum, also covered with an elastic membrane. By this means the pressure of the blood within the auricle or ventricle is communicated to the corresponding external drum. Upon each drum rests a light lever, in such a way that any increased pressure within the drum, which distends its elastic membrane, lifts at the same time the farther end of the lever. Consequently the oscillation of the two levers indicates the variations of pressure within the auricle and ventricle respectively.

The registering machine consists of a revolving cylinder or strip of paper, moving by clockwork at a uniform rate, with which the extremities of the levers are in contact, and upon which they trace corresponding lines. When the pressure in either cardiac cavity is uniform, its lever will trace upon the revolving cylinder a straight line; but whenever this pressure is increased the line will rise above the horizontal, and when it is diminished the line will sink to a corresponding level. The upward and downward slopes of the two tracings will therefore record the time, rapidity, force, and duration of all changes in pressure in the right auricle and right ventricle of the animal under observation.

Fig. 65.



Cardiographic Trace, showing variations of pressure during cardiac pulsations in the right auricle and right ventricle of the horse. *R A.* Tracing of right auricle. *o, o, o.* Maximum of pressure in auricular cavity. *R V.* Tracing of right ventricle. *x, x, x.* Maximum of pressure in ventricular cavity. (Marey.)

The tracings obtained by this method (Fig. 65) show that the contraction of the auricle precedes by a very short interval that of the

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* Physiologie Médicale de la Circulation du Sang. Paris, 1863, p. 54.

ventricle. It is also momentary in duration, the line, after reaching its maximum elevation, immediately descending nearly to its former level. Then follows a series of undulations, due to the vibration of the auriculo-ventricular valves, already closed by the contraction of the ventricle. The pressure in the relaxed auricle then slowly increases by the influx of blood from the great veins, until the time arrives for a second auricular contraction, when it suddenly rises to a maximum and again falls as before. The ventricular contraction, which follows almost immediately that of the auricle, is much more powerful, but requires a little longer interval to arrive at its maximum, and its entire duration is at least three times as long as that of the auricle. It will be seen that during the slow filling of the auricle with blood, a similar partial increase of pressure takes place in the ventricle; and the maximum pressure in the auricle corresponds in time, with a momentary undulation in the ventricle, immediately followed by the extreme rise of pressure, due to the ventricular contraction.

The exploration of the left cavities of the heart by these means, is much more difficult than that of the right, but Marey succeeded, in several experiments, in introducing pressure-tubes simultaneously into the right auricle and ventricle, through the jugular vein, and into the left ventricle through the carotid artery, and in ascertaining the comparative pressure in these cavities, as measured in millimetres of the mercurial column. In one instance the force indicated by the different pressure-gauges was as follows:

Pressure of Blood in the	
Right Auricle	2.5 mm.
Right Ventricle	25.0 "
Left Ventricle	128.0 "

The relation in force between the two ventricles varied somewhat in different animals, according to their bodily condition and the state of the circulation; but taking all the observations together, the force of pressure in the left ventricle was in general from three to five times greater than in the right.

The pressure to which the blood is subjected in the ventricles is therefore much greater than in the auricles; and it is prevented from reacting in a backward direction by the closure of the auriculo-ventricular valves. The force of the right ventricle is expended on the blood in its passage through the pulmonary artery and the pulmonary capillaries; while that of the left ventricle is sufficient for its propulsion through the general arterial system.

The Arterial Circulation.

The arteries are a system of branching tubes, which commence with the aorta and ramify throughout the body, distributing the blood to the peripheral vascular organs. They consist of three principal coats, namely, an *inner* coat, composed of thin elastic laminæ lined with flattened epithelium cells; a *middle* coat, containing elastic tissue and unstriped muscular fibres, arranged transversely around the vessel; and an *external* coat of condensed connective tissue. The principal difference between the larger and smaller arteries is in the structure of their middle coat. In the smaller arteries this is composed exclusively of muscular fibres. In arteries of medium size it contains both muscular and elastic tissue; while in those of the largest calibre it consists of elastic tissue alone. The large arteries, accordingly, have much elasticity and but little contractility; while the smaller are contractile, and less elastic.

Movement of Blood through the Arterial System.—The movement of the blood in the arteries is due to the impulse of the ventricular systole. The arterial system may be regarded as a great vascular cavity, subdivided by the successive branching of its vessels, but communicating freely with the heart at one extremity, and with the capillary plexus at the other. At the time of the heart's contraction, the muscular walls of the ventricle close upon its contents; and as the auriculo-ventricular valves shut back and prevent regurgitation, the blood is forced out from the ventricle through its arterial orifice. As the ventricle relaxes it is again filled with blood from the auricle, and delivers it, as before, by a new contraction, into the arteries. Under these recurring impulses the blood moves from the heart through the arterial system.

Arterial Pulse.—At each ventricular systole a charge of blood is driven into the arteries, distending them by the additional fluid forced into their cavities. When the ventricle relaxes, its distending force is suspended; and the elastic arterial walls, reacting upon their contents, would drive the blood back into the heart were it not for the closure of the semi-lunar valves, which prevent a backward movement. The blood is accordingly propelled, under the elastic pressure of the arterial walls, into the capillary system. When the arteries, thus partially emptied, have returned to their previous dimensions, they are again distended by another contraction of the heart. This produces, throughout the arterial system, a succession of expansions and reactions, known as the *arterial pulse.*

Since each arterial expansion is produced by a ventricular systole, the pulse, as felt in any superficial artery, is a convenient guide for ascertaining the character of the heart's action. The radial artery at the wrist, owing to its accessible situation, is usually employed for this purpose. Any variation in the frequency, force, or regularity of the heart's movement is indicated by a corresponding modification of the pulse at the wrist.

The average frequency of the pulse in man is, for the adult male in a state of quiescence, 70 beats per minute. This rate may be accelerated by muscular exertion. Even the variation of muscular effort between the standing, sitting, and recumbent postures, will make a difference in the frequency of the pulse of from 8 to 10 beats per minute. Age has a marked influence in the same direction. According to Carpenter, the pulse of the fœtus, before birth, is about 140, and that of the newly-born infant 130. During the first, second, and third years it gradually falls to 100; by the fourteenth year to 80; and is reduced to the adult standard by the twenty-first year. At every age, mental excitement may produce a temporary acceleration, varying in degree with the peculiarities of the individual.

As a rule, the rapidity of the heart's action is in inverse ratio to its force. A slow pulse, within physiological limits, is usually a strong one, and a rapid pulse comparatively feeble. This is especially noticeable in the lower animals, when the force of the heart's action is experimentally measured by the arterial impulse; an increased frequency of the cardiac pulsations being almost invariably accompanied by a diminution in their strength. The same is true in disturbance of the heart's action from morbid causes; the pulse in febrile or other debilitating affections becoming weaker as it grows more rapid. An excessive rapidity of the pulse is an indication of great danger, and, in the adult male, a continued rate of 160 per minute is almost invariably a fatal symptom.

Increased Curvature of the Arteries in Pulsation.—In the distension of the arteries under the force of the ventricular *systole*, these vessels are elongated as well as widened; and especially in those having a distinctly curvilinear or serpentine course, an elongation and consequent increase of curvature is observable at each pulsation. This may be seen in emaciated persons, in the temporal artery, or in the radial at the wrist, and is very marked in the mesenteric arteries in the abdomen of a quadruped. A superficial artery, running over a bony surface, may be partially lifted out of its bed from this cause, at each pulsation. In old persons the arterial curvatures become permanently enlarged from frequent distension; and all the smaller arteries tend to assume, with the advance of age, a more serpentine course.

Fig. 66.

Elongation and increased curvature of an Artery in Pulsation.

Characters of the Arterial Pulse.—The shock of an arterial pulsation, as perceived by the finger, varies a little in time, according to its distance from the centre of the circulation. If one finger be placed upon the chest over the heart's apex, and another over the carotid artery at the middle of the neck, little or no difference in time is perceptible between the two impulses; the distension of the carotid being sensibly simultaneous with the heart's contraction. But if the second finger be placed on the temporal artery, its impulse is felt to be a little later than that of the heart. The pulse of the radial artery at the wrist is also later than that of the carotid, and that of the posterior tibial at the ankle later than that of the radial. The greater the distance from the heart, the later is the pulsation of the artery.

But this difference in time of the arterial pulsations, in different parts of the body, is rather relative than absolute. The cardiac impulse is communicated at the same instant to every part of the arterial system, and the distension begins in all the arteries simultaneously; but it reaches its completion more rapidly in the neighborhood of the heart, more slowly at a distance. The arterial pulse, as perceived by the finger, marks the condition of *maximum distension ;* and this condition occurs at a later period, according to the distance of the artery from the heart.

The contraction of the left ventricle is a brisk and sudden motion. The blood driven into the arterial system, meeting with a certain resistance from that already in the vessels, does not instantly displace a quantity equal to its own, but a part of its force is expended in stretching the vascular walls. The expansion of the nearer arteries is therefore sudden and momentary, like the contraction of the heart. But it still requires a certain expenditure of time; so that, a little distance farther on, the vessel is not distended with the same rapidity, and the arterial dilatation arrives more slowly at its maximum.

On the other hand, at the moment of cardiac relaxation, the elastic reaction of the larger arteries propels a portion of blood into the smaller vessels beyond, and thus partially maintains their distension. In the larger arteries, accordingly, there is a noticeable difference in size between the periods of their expansion and collapse; since they are fully distended by the ventricular systole, and afterward emptied, in great measure, by their own reaction. But in the smaller arterial branches, this difference is not so marked. They are less fully distended at the time of the cardiac impulse, because this force is partly expended on the large vessels; and their subsequent reaction is less complete, because they are then subjected to the elastic pressure from the arterial trunks. This produces a gradual modification of the arterial pulse, from the heart toward the periphery.

The mechanism of this change is illustrated in the experiments of Marey,* by means of an elastic tube attached to a forcing pump, and open at its farther extremity. At different points on the tube are small levers, which are lifted by its distension when water is driven into it from the forcing pump. Each lever carries at its extremity a small pencil, which marks upon a strip of paper, moving with uniform rapidity, the curves of its elevation and depression. By these curves both the extent and rapidity of the distension of different parts of the tube may be registered, as shown in Fig. 67.

From this it appears that the distension produced by the stroke of the forcing pump begins at the same moment throughout the tube, and that the pulsation is everywhere of equal length. But near the commencement of the tube, its expansion is wide and sudden, lasting for only one-sixth part of the entire pulsation, while the remaining five-

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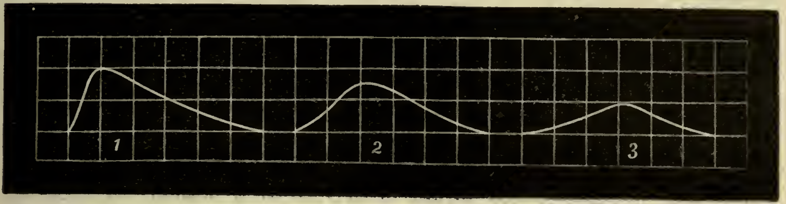
* Journal de la Physiologie. Paris, Avril, 1859.

sixths are occupied by its reaction. At more remote points the time of expansion becomes longer and that of collapse shorter; until finally, at a certain distance, the amount of expansion is reduced one-half, and the two periods are equalized in duration.

Fig. 67.



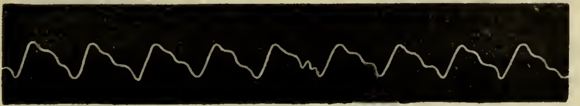
Curves of Pulsation in an Elastic Tube.—1. Near the distending force. 2. At a distance from it. 3. Still farther removed.

Registration of Pulse by the Sphygmograph.—The frequency and character of the arterial pulse may be permanently recorded by the use of an instrument similar in principle to the cardiograph, but adapted for application to an artery. This instrument, of which there are various modifications, is the *sphygmograph.* It consists essentially of a small ivory or metallic plate, gently pressed upon the artery by means of a fine spring, so as to rise and fall with the expansion and collapse of the arterial tube. The plate communicates its motion, through a vertical metallic rod, to a registering lever above. The oscillating extremity of the lever, when the instrument is in operation, thus indicates the movements of the artery, and marks upon a strip of paper the frequency and form of its pulsations.

The advantage of such an instrument is, first, that the length of the lever magnifies to the eye the extent of the arterial oscillations, and thus enables us to perceive movements too delicate to be distinguished by the touch; and, secondly, that, each part of a pulsation being permanently registered, the most momentary changes may be afterward studied at leisure and compared with each other.

By this means it has been shown, that, while there is a general resemblance in the form of pulsation of different arteries, nearly every vessel to which the instrument can be applied presents peculiarities dependent on its size, position, and distance from the heart. In the radial artery at the wrist, each pulsation consists of a sudden expansion of the vessel, indicated by a rapid upward movement of the lever, making, in the trace, a straight, nearly vertical line. This is fol-

Fig. 68.



Trace of the Radial Pulse, taken by the Sphygmograph.

lowed by a gradual descent corresponding with the collapse of the artery, until it reaches the lowest point of the trace, when the ascending movement again takes place, and so on alternately. The line of descent is marked by one, two, or three slight undulations, indicating a corresponding variation in the tension of the artery during its collapse.

These undulations in the line of descent, in the sphygmograph tracing, are due to an oscillation in the mass of the blood, subsequent to the impulse of the heart, and during the reaction of the arterial system. Marey* has shown that similar oscillations are produced when any incompressible liquid is driven by a sudden impulse into an elastic tube; and that they may be indicated by a similar movement of the index of a sphygmograph. When the heart's impulse is moderate, and the tension of the arterial system fully developed, the undulations in the descending line of the pulse are not very perceptible; but when the heart's impulse is more rapid, and the arterial tension diminished, the undulations become more marked. Traces of different form, in this respect, may be produced in the same individual by artificial variations in the temperature of the body. The following are three traces of the radial pulse obtained in his own person by Marey, by increasing the quantity of clothing at intervals of twenty minutes:

Fig. 69.

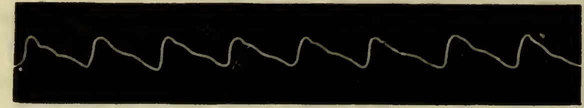


Fig. 70.

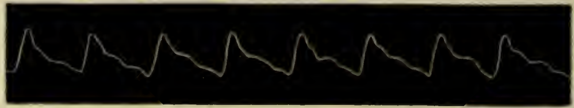
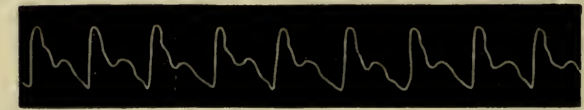


Fig. 71.



Variations of the Radial Pulse, under the influence of increased temperature. (Marey.)

Dicrotic Pulse.—In certain conditions, accompanied by rapid pulsation of the heart with diminished arterial tension, the secondary oscillation of the artery becomes so marked, in proportion to the original impulse, that it is perceived by the finger, and thus the pulse is apparently doubled; that is, there are two pulsations of the artery for each contraction of the heart, namely, one due to the original

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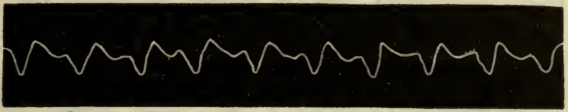
* Physiologie Médicale de la Circulation du Sang. Paris, 1863, p. 266.

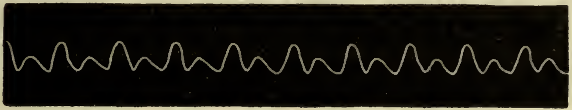
impulse, and another caused by the oscillation of blood in the feebly distended artery. This is the *dicrotic* pulse, often present in diseases of a typhoid character.

FIG. 72.



DICROTIC PULSE OF TYPHOID PNEUMONIA. (Marey.)

FIG. 73.



DICROTIC PULSE OF TYPHOID FEVER. (Marey.)

It is evident that the dicrotic character of the pulse is not altogether peculiar to diseased conditions, since it exists in some degree, as shown by the preceding figures, even in health. But it is usually too slight to be perceptible by the finger unless exaggerated from morbid causes.

The mechanism of the dicrotic pulse has been demonstrated by Koschlakoff.* If a liquid be driven by a sudden impulse through an elastic tube, connected with two separate pressure gauges, one near the point of entrance of the liquid, the other near its exit, the liquid will rise in the first gauge before the increased pressure reaches the second; it then falls while the second is rising, and again rises while the second falls; showing an alternate increase and diminution of pressure in the two extremities of the tube. This alternation continues until the pressure is equalized, or until the tube is again distended by a new impulse.

Pulsating Flow of Blood in the Arteries.—Owing to the alternate contraction and relaxation of the heart, the blood moves through the arterial system in a series of impulses; and in hemorrhage from a wounded artery the blood flows in successive jets, as well as more rapidly than if it came from veins or capillaries. If a slender canula be introduced through the walls of the left ventricle, in the exposed heart of a living animal, the flow of blood from its orifice is intermittent. A strong jet takes place at each ventricular contraction, and is interrupted at the time of relaxation. But if the puncture be made in a large artery near the heart, the blood is discharged from it in a continuous stream; only its flow is abundant at the time of ventricular contraction, and more scanty at the time of relaxation. The distension and elasticity of the arterial walls modify the effects of the separate arterial pulsations, and partially fuse them with each other; producing, in the larger and medium-sized arteries, a movement of the blood

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* In Lorain, Etudes de Médecine Clinique. Paris, 1870, p. 75.

which increases at each cardiac impulse, and diminishes during relaxation.

Equalization of the Blood-current in the Arterial System.—Since the distensible and elastic properties of the arterial walls make the flow of blood more continuous than it would otherwise be, this effect increases as the blood moves through the arterial system. A part of the force of each pulsation is absorbed, for the time being, in the distension of the artery, and is again returned in an impulse to the blood at the following interval, by the reaction of the vessel. The farther from the heart the blood recedes, the greater becomes the influence of the intervening arteries; and thus the remittent or pulsating character of the arterial current, which is strongly pronounced in the vicinity of the heart, becomes gradually diminished during its passage through the vessels, until in the smaller arteries it is hardly perceptible.

The influence of an elastic medium, in equalizing the flow of an interrupted current, may be shown by injecting water from a force-pump alternately through two tubes, one of India-rubber, the other of metal. Whatever be the length of the metallic tube, the water will be delivered from its extremity in distinct jets, corresponding with the strokes of the piston: but when it is replaced by an elastic tube of sufficient length, the separate impulses are merged into each other, and the water is discharged in a continuous stream.

The elasticity of the arteries never completely neutralizes the effect of the cardiac contractions, since a pulsation can be seen in the flow of blood in even the smallest arteries, when examined under the microscope; but it diminishes in degree from the heart outward, and the current becomes nearly continuous at the confines of the capillary system.

The Arterial Pressure.—The arterial circulation, as shown by the above facts, is the combined result of two different forces; namely, the contraction of the heart, by which the blood is propelled in successive impulses, and the elasticity of the arteries, by which it is subjected to a continuous pressure.

If one of the larger or medium-sized arteries be divided, in the living animal, and a glass tube of the same diameter fixed in its orifice in the vertical position, the blood will rise in the tube to a height of five and a half or six feet, and, until coagulation occurs, will continue to oscillate about this level. The column of fluid thus supported indicates the pressure to which the blood is subjected within the vessels. This force, due to the reaction of the arterial system, is known as the *arterial pressure.*

The arterial pressure is best measured by connecting an open artery, by means of a flexible tube, with a small reservoir of mercury, provided with a narrow upright graduated tube, open at its upper extremity. When the mercury in the reservoir is exposed to the pressure of the blood, it rises in the upright tube to a corresponding level.

The average arterial pressure, in the dog and other animals of similar size, is equivalent to a column of mercury 150 millimetres in height. But while, in such an instrument, connected with the arterial system, the mercurial column indicates on the whole an average pressure, it also exhibits two series of oscillations; showing a fluctuation in the degree of pressure, owing to two different causes.

One of these oscillations is synchronous with *respiration.* At every inspiration, the level of the mercury falls somewhat, with every expiration it rises. As the movement of inspiration consists in an expansion of the chest cavity, its effect is to diminish the pressure on the heart and great blood-vessels, and consequently to lower in a similar degree the tension of the whole arterial system. In expiration, on the other hand, the thoracic walls return to their former position, and the pressure on the organs within the chest is reëstablished. These changes are indicated by corresponding variations in the height of the mercurial column. The oscillations due to this cause, however, are not uniform, but vary according to the condition of the respiratory movements. When respiration is active and labored, they may reach the extent of 30 millimetres; when it is quiet, as in an animal deeply etherized, they may be nearly imperceptible.

The remaining oscillation is more uniform, and is due to the *cardiac pulsations.* It consists of comparatively rapid undulations of the mercurial column, simultaneous with the movements of the heart. At every ventricular contraction the mercury rises 12 or 15 millimetres, and at every relaxation falls to its previous level. The instrument thus indicates the intermitting pressure of the heart's action; and has accordingly received the name of the *cardiometer.* As the average height of the column in the cardiometer is 150 millimetres, and as it varies by 15 millimetres under the influence of the cardiac pulsations, it appears that each contraction of the heart is superior in force to the resistance of the arteries by about one-tenth; and the arterial system is, therefore, kept full, and the arterial tension maintained, notwithstanding the constant discharge of blood into the capillaries.

Rapidity of the Arterial Current.—The blood moves in the arteries more rapidly than in any other part of the vascular system. Its exact rate varies according to the situation of the vessel and the period of the pulsation; being greatest in the immediate neighborhood of the heart, and diminishing from this point outward. The division of the arterial trunks into branches and ramifications increases their surface of contact with the blood; and the increased adhesion produced by this contact retards the current, which is accordingly slower in the small arteries than in those of large or medium size. In the smallest arteries, as seen under the microscope in the transparent tissues, the partial adhesion of the blood to the vascular wall, and the greater rapidity of its flow in the axis of the vessel are readily perceptible. The consistency of the circulating fluid, however, and the smoothness of the internal surface of the arteries, are such that this obstacle to the movement of the blood has only a partial retarding influence; and even in the smallest arteries its flow is so rapid that the separate blood-globules cannot be distinguished, but only a mingled current shooting forward with increased velocity at each pulsation.

The average rapidity of the blood stream in the larger arteries, in dogs, horses, and calves, was determined by Volkmann, as 30 centimetres per second. The most exact experiments on this point are those of Chauveau,* who introduced into the carotid artery of the horse a thin brass tube, about five centimetres long and eight or nine millimetres in diameter. The tube was introduced through a longitudinal incision in the walls of the vessel, and secured by a ligature near each extremity; so that the arterial current might pass, without serious obstruction, through the tube forming, for the time, a part of the arterial walls. In the side of the tube was a small opening, three millimetres long by one and a half millimetre wide, closed by an elastic membrane, so secured as to prevent the escape of blood. Through the centre of the membrane was passed a light metallic needle, the inner extremity of which, somewhat flattened in shape, received the impulse of the blood; while the outer portion, prolonged into a slender index, marked upon a semicircular scale the oscillations of the inner extremity, and consequently the varying rapidity of the arterial current. The actual velocity, indicated by any given oscillation of the needle, was ascertained beforehand by attaching the apparatus to an elastic tube and passing through it a stream of warm water of known rapidity.

The details of the circulatory movement, as indicated by these experiments, differ somewhat in the larger and the smaller arteries.

a. In the carotid artery, at the instant of ventricular systole, the blood is suddenly put in motion with a high velocity, amounting on the average to a little over 50 centimetres per second.

At the termination of the systole, and immediately before the closure of the aortic valves, the movement of the blood decreases considerably, and may even, for the time, be completely arrested.

At the instant of closure of the valves, the circulation receives a new impulse, and the blood again moves forward with a velocity of rather more than 20 centimetres per second.

Afterward, the rapidity of the current gradually diminishes during the heart's inaction, until, at the end of this period and just before a new systole, it is reduced, on the average, to 15 centimetres per second.

b. In the smaller arteries, such as the facial, the movement of the blood is more uniform. At the moment of the heart's systole it is less rapid than in the carotid; and on the other hand, it has a greater velocity during the period of ventricular repose. The secondary impulse, following the closure of the aortic valves, is less perceptible than in the larger arteries, and may even be altogether absent.

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* Journal de la Physiologie. Paris, Octobre, 1860, p. 695.

The Venous Circulation.

The veins, like the arteries, are composed of three coats—an inner, middle, and exterior; but they contain a smaller quantity of muscular and elastic fibres, and a larger proportion of condensed connective tissue. They are consequently more flaccid and compressible than the arteries, and less elastic and contractile. They are furthermore distinguished, in the limbs, neck, and external parts of the head and trunk, by being provided with valves, in the form of festoons, so placed that they allow the blood to pass from the periphery toward the heart, but prevent its reflux in the opposite direction.

Though the walls of the veins are thinner and less elastic than those of the arteries, yet their capacity for *resistance to pressure* is equal, or even superior. Milne Edwards* has collected the results of various experiments, which show that the veins will sometimes bear a pressure sufficient to rupture the arteries. In one instance the jugular vein supported a pressure equal to a column of water 148 feet in height; and in another, the iliac vein of a sheep resisted a pressure of more than four atmospheres. The portal vein resisted a pressure of six atmospheres; and in one case, in which the aorta of a sheep was ruptured by a pressure of 72 kilogrammes, the vena cava of the same animal supported a pressure of 80 kilogrammes.

This property of the veins is due to the white fibrous tissue in their composition; the same tissue which forms nearly the whole of the tendons and fasciæ, and which is distinguished by its density and unyielding nature.

The *elasticity* of the veins, on the other hand, is much less than that of the arteries, and there is consequently but little variation in their calibre. When filled with blood, they swell to a certain size; when empty, their sides collapse, and remain in contact with each other.

Another peculiarity of the venous system consists in its numerous *communicating channels.*

In injected preparations, two, three, or more veins are often seen coming from the same region, with frequent transverse communications. The deep veins accompanying the main arteries of the limbs inosculate freely with each other, and also with the superficial veins. Among those coming from the head, the external jugulars communicate with the thyroid, the anterior jugular, and the brachial veins. The external and internal jugulars communicate with each other, and the two thyroid veins form an abundant plexus in front of the trachea.

Thus the blood, coming from the periphery toward the heart, flows in a number of communicating channels; through which it passes, under different conditions of pressure, by a variety of routes, but always in the same direction.

Movement of the Blood through the Venous System.—The flow of

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* Leçons sur la Physiologie. Paris, 1859, tome iv., p. 301.

blood through the veins is less powerful and regular than that through the arteries. It depends on the action of three different forces.

I. The most important of these forces is the *pressure from the capillary circulation.* The blood moves from the arteries into and through the capillary vessels, under an impulse derived originally from the heart, and afterward replaced by the comparatively uniform arterial pressure. This pressure is not entirely exhausted in the capillaries; and the blood accordingly emerges from these vessels and enters the venous system with a force sufficient to fill its rootlets, and to pass thence into its larger branches and trunks. As the veins converge from the periphery toward the centre, and unite into trunks of larger calibre, their extent of contact with the circulating fluid, and their resistance to its movement, constantly diminishes; while the contractions of the right ventricle relieve the returning current from the obstacle of its accumulation. The continuous pressure of the blood from the capillaries thus supplies an effective cause for its movement through the veins.

Fig. 74.

Vein with valves open.

Fig. 75.

Vein with valves closed; stream of blood passing off by a lateral channel.

II. The flow of blood through the veins is aided in great measure by the *contraction of the voluntary muscles.* The veins in the limbs, and in the parietes of the head and trunk, lie among voluntary muscles which are often in a state of alternate contraction and relaxation. At each contraction the muscles become swollen laterally, thus compressing the veins between them. As the blood, expelled by this pressure, cannot regurgitate toward the capillaries, owing to the closure of the venous valves, it is forced onward toward the heart; and when the muscle relaxes and the vein is liberated from pressure, it is again filled from behind, and the circulation goes on as before.

The muscular system acts in this way by communicating to the venous current indirect impulses of frequent repetition, which, combined with the action of the valves, urge the blood from the periphery toward the heart.

III. A third cause, contributing to the movement of the venous blood, is the *force of aspiration* exerted by the thorax. The expansion of the chest in inspiration diminishes the pressure upon its contents, and consequently tends to draw into the thorax any fluids which can gain access to it. The expanded cavity is principally filled by the entrance of atmospheric air through the trachea and bronchi. But the blood in the neighboring veins is solicited at the same time in a similar direction. The influence of this force extends indirectly throughout the venous system, each expansion of the chest diminishing the resistance at the centre of the circulation, and thus causing an increased flow toward the intra-thoracic veins, while the remainder are filled from behind as they are emptied in front.

Rapidity of the Venous Current.—With regard to the rapidity of the venous current, no results have been obtained by direct experiment. Owing to the flaccidity of the veins, and the readiness with which the flow of blood through them is disturbed, it is not possible to determine this point, in the same manner as for the arteries. But a calculation has been made, based on the comparative capacity of the arterial and venous systems. As the blood which passes outward through the arteries returns through the veins, the rapidity of its flow in each direction must be in inverse ratio to the capacity of the vessels. The entire venous system, when distended by injection, contains about twice as much fluid as the arteries. During life, however, the venous system is at no time so completely filled with blood as the arteries; and, allowing for this difference, it may be estimated that the entire quantity of venous blood is to the entire quantity of arterial blood nearly as three to two. The velocity of the blood in the veins, as compared with that in the arteries, is therefore as two to three; and if we regard the average rapidity of the arterial current, according to Volkmann's experiments, as 30 centimetres per second, this would give the movement of blood in the veins as about 20 centimetres per second. This estimate, however, is only approximative; since the venous circulation varies, according to many circumstances, in different parts of the body. It may nevertheless be considered as expressing with sufficient accuracy the general relative velocity of the arterial and venous currents in corresponding parts of their course.

The Capillary Circulation.

The capillary blood-vessels are minute inosculating tubes, which permeate the vascular organs, and bring the blood into close proximity with their tissues. They are continuous, on the one hand, with the terminal ramifications of the arteries, and, on the other, with the commencing rootlets of the veins. They vary somewhat in size in different tissues, their average diameter in man being about 10 mmm., or $\frac{1}{100}$ of a millimetre. According to Kölliker, the largest capillaries are in the glands and the osseous tissue, where they reach the diameter of 15 mmm.; while the smallest, in the muscles, the nerves, and the retina, are 4.5 mmm., that is, almost exactly the size of the smallest of the red globules of the blood.

As the arterial ramifications approach the capillary system, they diminish in size, and lose their external coat of connective tissue. Their middle coat is, at the same time, reduced to a single layer of fusiform muscular fibres, which become gradually less numerous, and at last disappear altogether. The vascular canal is thus finally composed only of a single tunic continuous with the internal coat of the arterial ramifications.

The capillary blood-vessel, in its recent condition, when extracted from any soft vascular tissue, appears to consist of a simple, nearly homogeneous tubular membrane, with flattened oval nuclei placed at short distances from each other, and projecting slightly into its cavity. But if the vessel be treated with a weak solution of silver nitrate, its inner surface becomes marked off into regular spaces, each of which includes a nucleus; indicating that its apparently homogeneous tunic is composed of flattened epithelium-like cells, united with each other at their adjacent edges by an intervening cement. It is this intervening substance which becomes darkened by silver nitrate, bringing into view the outlines of the epithelium cells of the vascular wall.

Fig. 76.

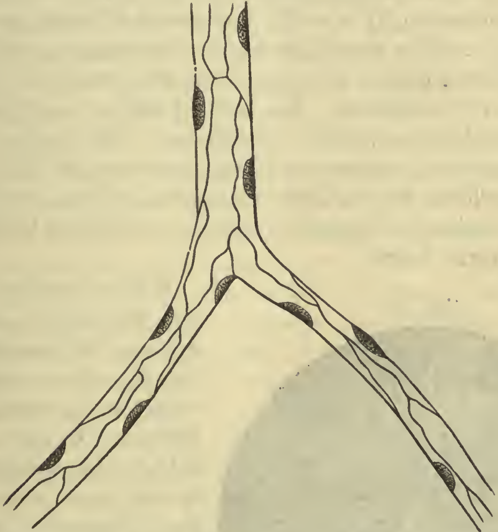
Small Artery with its muscular tunic (*a*), breaking up into capillaries. From the *pia mater*.

The form of the cells varies in different regions and in capillaries of different calibre. According to Kölliker, in the smaller capillary blood-vessels, from 4.5 to 7 mmm. in diameter, they are narrow, elongated, and fusiform, as in Fig. 77; often curled from side to side, so as to form each a half cylinder, two of them joining at their edges to complete the capillary tube, and intercalated at their ends between the adjacent cells. In the larger capillaries, from 8 to 15 mmm. in diameter, the cells are shorter and wider, like those of ordinary pavement epithelium. Owing to this structure of the capillary blood-vessels, the vascular system, in the opinion of some histologists, is to be regarded as a series of intercellular canals, provided, in different regions, with additional layers of muscular, elastic, or connective tissue.

The capillary blood-vessels are distinguished by their frequent inosculation. The arteries divide and subdivide, as they pass from within outward, while the veins as constantly unite with each other, to form larger branches and trunks, from the periphery toward the centre; and although the arteries always present inosculation in certain regions, and the veins more frequently still, this is, nevertheless, a secondary feature in both vascular systems. The arteries are essentially diverging tubes to distribute the blood from within outward; the veins are converging channels to transport it from without inward.

The capillaries, on the other hand, are mainly characterized by their constant and repeated intercommunication; uniting with each other at such short intervals, as to form an interlacing network, known as the *capillary plexus.* The vessels of the plexus vary somewhat in size, number, and arrangement in different parts; but in every vascular tissue there are certain spaces or islets, surrounded by the capillaries, and into which they do not penetrate. Such intervascular spaces must therefore obtain their nourishment by exudation and absorption through the capillary walls and the intervening tissue.

FIG. 77.



CAPILLARY BLOOD-VESSEL, from the tail of the tadpole; showing the outlines of its epithelium-like cells, rendered visible by the action of silver nitrate. (Kölliker.)

The special arrangement of the capillary blood-vessels, and the form and size of the meshes of their network, are, in general, characteristic of each organ and tissue. In the muscles, the intervascular spaces are long parallelograms, corresponding with the muscular fibres; in the mucous membrane of the stomach, they are hexagonal or irregularly circular, inclosing the orifices of the gastric follicles; in the papillæ, of the tongue and skin, and in the placental tufts, the capillaries form twisted vascular loops; in the glomeruli of the kidneys, convoluted coils; in the connective tissue, irregularly shaped figures, like those included by the fibrous bundles which they supply.

The capillary blood-vessels are most abundant, and connected by the closest inosculations in organs where the blood serves for other purposes than local nutrition; such as aeration, secretion, or absorption. One of the finest capillary networks is that of the lungs, in which the diameter of the intervascular spaces is sometimes a little greater and sometimes a little less than that of the capillaries themselves. In the intra-lobular plexus of the liver, they are only a little wider than the vessels forming the network. In the nerves, the serous membranes and the tendons, on the other hand, the capillaries are less closely interwoven; and in the adipose tissue they form wide meshes, embracing the fat vesicles.

Movement of the Blood in the Capillary Vessels.—The motion of the blood through the capillaries may be studied, under the microscope, in any transparent tissue of sufficient vascularity. The frog is the most convenient animal for this purpose, owing to the readiness with which the circulation will go on in the exposed organs at ordinary temperatures. To secure immobility, the brain and medulla oblongata should be broken up by a needle introduced through the cranium, or the voluntary muscles paralyzed by the subcutaneous injection of six drops of a filtered watery solution of woorara, made in the proportion of one part to five hundred. The body should be enveloped in a loose, moistened bandage, to prevent desiccation. The tongue, the web of the foot, the pulmonary membrane, the mesentery or the bladder may be used to exhibit the capillary circulation, which, with the aid of appropriate mechanical appliances, may be maintained in either of these regions for several hours.

When examined in this manner, the smaller arterial ramifications, the capillary vessels, and the minute veins are often visible in the same tissue. The blood can be seen entering the field by the arteries, shooting through them with great rapidity in successive impulses, and flowing off more slowly by the veins. In the capillary plexus it moves with a uniform current, considerably less rapid than in either the arteries or the veins. A further peculiarity of the capillary circulation is that it has no definite origin or termination, but represents a movement of the blood through all parts of the tissue. Its streams pass indifferently above and below, at right angles to each

Fig. 78.

Capillary Circulation in web of frog's foot.

other, or even in opposite directions; penetrating everywhere the substance of the organ with a kind of vascular irrigation.

The motion of the red and white globules is also peculiar, and shows distinctly the difference in their physical properties. In the larger vessels the red globules are carried along in close column, in the central part of the stream; while near the edges there is a transparent space occupied by clear plasma, in which no red globules are visible. In the smaller vessels the globules pass two by two, or follow each other in single file. Their flexibility and semi-fluidity are very apparent as they are folded, bent or twisted, or made to glide through branches of communication, smaller than themselves. The white globules, on the other hand, move more slowly. They drag along the external portions of the current, and are sometimes arrested for a few seconds, adhering to the inner surface of the vessel. Wherever the current is obstructed or retarded, the white globules accumulate and become for the time more numerous in proportion to the red.

It is during its passage through the capillaries that the blood serves for the nourishment of the tissues, and for absorption, secretion, or elimination. The tenuity of the vascular walls, their extent of surface in proportion to the blood which they contain, and the multiplication of the currents due to their division and inosculation, all contribute to this result, and make these vessels the most important physiological division of the circulatory system. The nutritious ingredients of the blood transude through their walls, and are appropriated by the tissues beyond. In the glandular organs they supply the substances requisite for secretion; in the villi of the intestine they take up the elements of the digested food; in the lungs they absorb oxygen and exhale carbonic acid; and in the kidneys they discharge the products of destructive assimilation, collected from other parts. The capillary circulation thus furnishes, directly or indirectly, the materials for the growth and renovation of the entire body.

Physical Cause of the Capillary Circulation.—The conditions which influence the movement of the blood in the capillaries are somewhat different from those of the arterial and venous circulations. By the successive division of the arteries from the heart outward, the movement of pulsation is to a great extent equalized in their smaller branches. But in the neighborhood of the capillary system, they suddenly break up into a terminal ramification of still smaller vessels, and so lose themselves at last in the capillary network. By this final increase of the vascular surface, the equalization of the heart's action is completed. There is no longer any pulsating character in the force which acts on the circulating fluid; and the blood moves through the capillary vessels under a continuous and uniform pressure.

This pressure is sufficient to propel the blood through the capillary plexus into the veins. The fact was first demonstrated by Sharpey, who employed an injecting syringe with a double nozzle, one of its extremities being connected with a mercurial gauge, while the other was inserted into the artery of a recently-killed animal. When the syringe, filled with defibrinated blood, was fixed in this position, it would press with equal force on the mercury in the gauge and on the fluid in the blood-vessels; and the height of the mercurial column would indicate the pressure required to carry the blood through the capillaries, and to return it by the corresponding vein. With one end of the injecting tube attached to the mesenteric artery of the dog, a pressure of 90 millimetres of mercury caused the blood to pass through the double capillary system of the intestine and the liver; and under a pressure of 130 millimetres, it flowed in a full stream from the extremity of the vena cava.

We have obtained similar results by experimenting on the blood-vessels of the limbs. A full grown healthy dog was killed, and one of the hind legs immediately injected with defibrinated blood, by the femoral artery, to prevent coagulation in the small vessels. A double syringe, filled with defibrinated blood, was then attached by one of its extremities to the femoral artery and by the other to a cardiometer. On making the injection, the defibrinated blood was returned from the femoral vein in a continuous stream under a pressure of 120 millimetres, and was very freely discharged under a pressure of 130 millimetres.

Since the arterial pressure during life is equal to 150 millimetres of mercury, it is evidently sufficient to account for the capillary circulation.

The capillaries have also a certain degree of elasticity; and they are furthermore surrounded, in many organs, by tissues which are themselves elastic. The effect of this property, in the vessels and neighboring parts, may be seen in artificial injections, not only of a lower limb through the femoral artery, but also of the liver through the portal vein. If, while the parts are distended by the fluid in their vessels, the injecting force be suddenly arrested, the current does not at once cease, but the fluid of injection continues to escape for some seconds from the femoral or hepatic vein. The elasticity of the surrounding tissues supplements that of the blood-vessels, and aids in producing a uniform movement in the capillary circulation.

Velocity of Blood in the Capillaries.—The rate of movement in the capillary circulation may be measured, with some precision, in the microscopic examination of transparent tissues. The results obtained in this way by different observers (Valentin, Weber, and Volkmann), show that the rate of movement of the blood through the capillaries is rather less than one millimetre per second. Since the rapidity of the current must be in inverse ratio to the calibre of the vessels through which it moves, it appears that the united calibre of all the capillaries must be not less than 300 times greater than that of the arteries. It does not follow from this that the whole quantity of blood contained in the capillaries at any given time is greater than that in the arteries; since, although the united *calibre* of the capillaries is large, their *length* is very small. The structure of the capillary system is such as to disseminate a small quantity of blood over a large space, allowing its physiological reactions to take place with rapidity and energy. Although the movement of the blood in these vessels, accordingly, is slow, yet as the distance between the arteries and the veins is very small, it requires but a short time for the blood to traverse the capillary system, and commence its returning passage by the veins.

General Rapidity of the Circulation.

The rapidity with which the blood passes through the *entire round of the circulation* has been demonstrated by Hering, Poisseuille, Matteucci, and Vierordt in the following manner: A solution of potassium ferrocyanide was injected into the right jugular vein of the horse, at the same time that a ligature was placed on the corresponding vein of the opposite side, and an opening made in it above the ligature. The blood flowing from this opening was received in separate vessels, at intervals of five seconds, and afterward examined. The blood drawn from the first to the twentieth second contained no trace of the ferrocyanide; but that which escaped from the twentieth to the twenty-fifth second showed unmistakable evidence of its presence. During this time therefore the foreign salt must have passed from the point of injection to the right side of the heart, thence through the pulmonary circulation to the left side of the heart, outward by the arteries to the capillaries of the head and neck, and thence down toward the heart by the opposite jugular vein.

Further observations have shown that the duration of the circulatory movement varies somewhat in different animals; being, as a general rule, longer in those of larger size. Their main result, as given by Milne Edwards,* is as follows:

Duration of the Circulatory Movement.

In the Horse	28 seconds.
" Dog	15 "
" Goat	13 "
" Rabbit	7 "

In experimenting on the dog, by injecting a solution of potassium ferrocyanide into the jugular vein, and immediately drawing blood from the corresponding vein on the opposite side, we have found that the short time required for closing the first vein by ligature after making the injection, and opening the second to obtain a specimen of blood, is sufficient for the passage of the ferrocyanide. If we regard the duration of this movement in man as intermediate between that in the dog and the horse, according to the difference in size, this would give the time required by the blood to make the complete circuit of the vascular system as not far from 20 seconds.

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* Leçons sur la Physiologie. Paris, 1859, tome iv., p. 364.

Local Variations in the Capillary Circulation.

Fig. 79.

Diagram of the Circulation.—1. Heart. 2. Lungs. 3. Head and upper extremities. 4. Spleen. 5. Intestine. 6. Kidney. 7. Lower extremities. 8. Liver.

An important class of phenomena connected with the capillary circulation consists of its local variations. These variations are often very marked, and show themselves in many different parts of the body. The pallor or suffusion of the face from mental emotion, the congestion of the glands and mucous membranes during digestion, and the defined redness of the skin after irritating applications, are instances of this kind. They are due to the varying condition of the smaller arterial branches which contract or dilate after different nervous influences, and thus diminish or increase the quantity of blood in the capillary circulation. When contracted, they resist the impulse of the arterial current, and admit the blood in smaller quantity. When dilated, they allow it a free access, and the blood passes in greater abundance to the capillary vessels.

These changes are most distinctly manifested in the periodical congestion of the glandular organs. All the glands and mucous membranes of the digestive apparatus enter into a state of vascular excitement at the time of secretion and digestion. This unusual vascularity can be seen, in the living animal, in the pancreas, and in the mucous membranes of the stomach and small intestine; which are visibly redder and more turgid during digestion and absorption than in the fasting condition.

The variations of the capillary circulation, as influenced by glandular activity and repose, have been most successfully studied in the submaxillary gland of the dog. While this gland is in active secretion the quantity of blood passing through its vessels is largely increased. In the experiments of Bernard * the submaxillary vein, during the condition of glandular repose, yielded five cubic centimetres of blood in a little more than one minute; but

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* Leçons sur les Liquides de l'Organisme. Paris, 1859, tome ii., p. 272

when the organ was excited to functional activity, it discharged the same quantity in fifteen seconds. Thus the volume of blood passing through the gland in a given time was more than four times as great while in active secretion as in a condition of repose.

The increased flow of blood, in a secreting gland, is accompanied by in important change in its appearance. During repose, the blood, which enters the submaxillary gland bright red, is changed from arterial to venous, and passes out by the veins of a dark color. But during active secretion, the blood is not only discharged in larger quantity, but passes out by the veins of a red color, hardly distinguishable from that of arterial blood. When the secretion of the gland is suspended, its venous blood again becomes dark-colored as before. There is little doubt that the same is true of other glands, and that the blood circulating in their capillaries is changed from red to blue only during the period of functional repose; while at the time of active secretion it passes through the vessels in greater abundance, and retains its ruddy color in the veins.

This variation depends on the different functions performed by the blood in the two periods. During glandular repose it serves for the usual changes of nutrition, which consume its oxygen, and consequently change its color from red to blue. But during active secretion the blood passes in larger quantity, while its watery and saline ingredients exude into the secretory ducts, bringing with them the materials accumulated in the intervals of repose; and as there is nothing in this process to exhaust the oxygen of the blood, it therefore passes out by the veins with its color comparatively unaltered.

A similar ruddy color of the blood is to be seen in the renal veins, where it is often nearly identical with that of arterial blood. When the kidneys are in a state of functional activity, the difference in color between the renal veins and those of the neighboring muscles, or the vena cava, is very marked. The only important change in the blood while passing through the kidneys is the elimination of its urea; the process of local nutrition being altogether secondary. Consequently the blood loses but little oxygen in these organs, and suffers but little alteration of its hue.

On the other hand, the venous blood coming from the muscles is very dark, especially if they be in a state of active contraction; and as the muscles form so large a part of the mass of the body, their condition has a preponderating influence on the color of the venous blood in general. The greater the activity of the muscular system, the darker is the blood returning from the trunk and extremities. In a state of repose or paralysis, on the contrary, the change is less marked; and in the complete relaxation produced by abundant hemorrhage or profound etherization, the blood in the larger veins often approximates in color to that in the arteries.

Finally, in the lungs the reverse process takes place. In these organs the blood is supplied with a fresh quantity of oxygen, to replace that consumed elsewhere; and accordingly it changes its color from dark purple to bright red while passing through the pulmonary capillaries.

Both the simpler and the more important phenomena of the circulation vary therefore at different times and in different organs. The blood has a different composition as it returns from different parts, or has been employed in different functions. In the parotid gland it yields the ingredients of the saliva; in the kidneys those of the urine. In the portal vein it contains the products of intestinal digestion; and in the hepatic vein it has suffered a further alteration by passing through the capillaries of the liver. In the lungs it changes from blue to red, and in the greater part of the general system, from red to blue; and even its temperature varies in different veins, according to the special nutritive changes in the organs from which they come.

CHAPTER VII.

THE LYMPHATIC SYSTEM.

IN addition to the series of connected canals, through which the blood passes in a continuous round by the arteries, capillaries, and veins, there is also a system of vessels, leading from the periphery toward the centre, and discharging into the great veins near the heart the materials which have been absorbed from the tissues. The fluid in these vessels is nearly colorless, and from its transparent and watery appearance is called the "lymph," the vessels themselves constituting the *lymphatic system.*

As the blood moves through the capillaries under the influence of the arterial pressure, certain of its ingredients transude through the vascular walls and penetrate the interstices of the tissues. An increased pressure of the blood, either from arterial congestion or from obstruction to the venous current, will increase the amount of transudation, producing an œdematous condition, which is first perceptible in the loose connective tissue, but which may afterward involve the more compact substance of the organs. In the normal state of the circulation, this interstitial fluid, which is the source of nutriment for the solid parts, is renewed by continual change. As fresh supplies are drawn from the circulating blood, the older portions are removed by absorption and returned to the centre of the circulation by the lymphatic vessels. Thus these vessels may be considered as complementary in function to the veins. The blood, containing the red globules, is rapidly returned to the lungs by the veins, to regain the necessary oxygen; while the lymphatic vessels collect more gradually the fluids which have served for nutrition and growth.

General Structure and Arrangement of the Lymphatic System.

In structure the lymphatics do not essentially differ from the blood-vessels, their main peculiarity being the greater delicacy and transparency of their walls. Those of larger and medium size consist of three coats, similar in general character to the corresponding tunics of the blood-vessels. According to Kölliker, the external coat alone is distinguished from that of the veins by the presence of muscular fibres arranged in a longitudinal and oblique direction; as seen in lymphatics of 0.2 millimetre in diameter and upward. Like the veins, they are provided with numerous valves, opening toward the heart and closing toward the periphery. The smallest lymphatic vessels have only a single coat, composed of flattened, epithelium-like, nucleated cells, which may be brought into view, like those of the capillary blood-vessels, by the staining action of silver nitrate.

Origin and Course of the Lymphatic Vessels.—So far as the origin of the lymphatic vessels has been demonstrated by injections, they commence by irregular plexuses. They are more abundant in organs which are well supplied with blood-vessels, and are absent in non-vascular tissues, such as those of the cornea, the vitreous body, and the epidermic and epithelial layers of the skin and mucous membranes. According to Recklinghausen, the meshes of the lymphatic plexus are usually intercalated between those of the capillary blood-vessels; so that the point of junction of two or more lymphatics is in the middle of the space surrounded by the adjacent blood-vessels. Thus the lymphatic capillary is situated at the greatest possible distance from the nearest capillary blood-vessels; and in the transudation of fluids from one to the other, the intervening tissue is completely traversed by the nutritious ingredients of the blood. In membranous expansions presenting a free surface, as in the skin and mucous membranes, the capillary blood-vessels are situated near the surface, while the lymphatics occupy a deeper plane. In the villi of the intestine, the network of blood-vessels is immediately beneath the epithelial layer, and the lacteal vessel in the central part of the villus.

Beside the lymphatic capillaries proper, certain irregularly-shaped spaces or canals, containing a colorless serous fluid, have been found in organs composed of dense connective tissue, like the central tendon of the diaphragm and muscular fasciæ. They are generally demonstrated by treating the tissues with silver nitrate, which stains the solid portions of a dark color, but leaves the capillary vessels and serous canals uncolored. These interstitial canaliculi are regarded by some observers as continuous with the lymphatic capillaries, and as the immediate sources of supply for the lymph. They are distinguished from the lymphatic capillaries by their smaller size, and by the fact that they are not provided with an epithelial lining.

From their plexuses of origin the lymphatic vessels pass inward to the great cavities of the body, uniting into branches and trunks, and following generally the course of the principal blood-vessels. Those of the lower extremities enter the abdomen and join the abdominal lymphatics, to form the commencement of the thoracic duct. This duct ascends, through the chest, to the root of the neck, where it is joined by lymphatics from the left side of the head and the left upper extremity, and terminates in the left subclavian vein, at its junction with the left internal jugular. The lymphatic vessels coming from the right side of the head and neck and the right upper extremity form the right lymphatic duct, which terminates in the right subclavian vein at its junction with the right internal jugular. Thus the lymph, collected from the vascular tissues of the entire body, is mingled with the venous blood a little before its arrival at the right side of the heart.

The Great Serous Cavities are Lymphatic Lacunæ.—In the amphibious reptiles there are irregularly-shaped spaces or lacunæ, forming part of the lymphatic system and interposed between adjacent organs in various parts of the body. In the mammalia the peritoneal and pleural cavities, and probably all the principal serous sacs, are also in communication with the lymphatic vessels. This was first shown by Recklinghausen* in the rabbit, by injecting the peritoneal cavity with milk, or a watery fluid holding granules of coloring matter in suspension, after which the lymphatic vessels of the central tendon of the diaphragm were found filled with the injection. Furthermore, the central tendon of the diaphragm being removed from the recently-killed animal, and a drop of milk placed upon its peritoneal surface, the milk globules could be observed under the microscope, running in converging currents to certain points on the surface of the tendon and thence penetrating into its lymphatic vessels. The cavity of the pleura has been found by similar means to communicate with the lymphatic vessels in its neighborhood. The serous cavities accordingly are either extensive lacunæ, forming in some regions the origin of the lymphatics, or else they are wide and shallow expansions, situated at various points in the course of these vessels.

The Lymphatic Glands.—During the passage of the lymphatic vessels from the periphery toward the centre, they are repeatedly interrupted by ovoidal gland-like bodies, of a pale reddish color, varying, in man, from two to twenty millimetres in their long diameter. They do not exist in fish and reptiles, but are always present in birds and mammalia. As a rule, each gland receives several lymphatic vessels, coming from the periphery; and several others leave it at the opposite surface, continuing their course toward the centre of the circulation. The former are called the "afferent," the latter the "efferent" lymphatic vessels. The lymphatic glands have no excretory duct, and whatever new materials they produce must be carried away either by the veins or by the efferent lymphatic vessels.

The lymphatic glands consist, first, of an external fibrous envelope, with prolongations from its internal surface in the form of septa and branching bands, dividing the interior into smaller spaces by their inosculation. The fibrous bands composing this framework are the "trabeculæ." Secondly, in the interstices between the trabeculæ is contained the pulpy substance of the gland. Thirdly, the blood-vessels in the interior of the gland follow distinct routes in the spaces between the trabeculæ. They are surrounded and held in position by fine branching fibres attached to their external surface; and in the meshes of these fibres, as well as between the blood-vessels, are imbedded a great number of rounded, granular, nucleated cells, about 9 mmm. in diameter, similar to the white globules of the blood and lymph, and known in this situation as "lymph globules." The presence of these cells, between and immediately around the capillary blood-vessels, gives to

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* Stricker's Manual of Histology, Buck's Edition. New York, 1872, p. 221.

the parts occupied by them a well-marked opaque appearance; and they thus form, in a thin section of the gland, elongated, opaque tracts, separated by transparent interspaces, and communicating with each other at frequent intervals. These tracts are called the *medullary cords* of the lymphatic gland. They are the only vascular parts of the organ; as the capillary blood-vessels never pass beyond them into the intervening transparent spaces. The transparent spaces are the *lymph-paths*, or the channels by which the lymph traverses the gland from its afferent to its efferent vessels. The afferent lymphatic vessels, according to the testimony of nearly all observers, after ramifying upon the outer surface of the gland, penetrate its fibrous envelope and become continuous with the transparent portions of its substance. This is shown by injections of the gland from the afferent vessels; and Kölliker has demonstrated a connection of the same channels with the efferent vessels, by injecting them from the substance of the gland.

The cause of the transparent appearance presented by the lymph-paths in thin sections of the gland is that their lymph-cells are easily detached by manipulation, while those of the medullary cords are more firmly fixed in the fibrous mesh-work and do not so readily yield to a displacing force. It has been found by Kölliker that a watery or serous fluid, injected through the substance of the gland under moderate pressure, will also displace these cells and leave the parts which they occupied nearly clear. It is for this reason that the lighter spaces in the lymphatic glands are regarded as the channels by which the lymph passes from the afferent to the efferent vessels, the lymph-cells being detached by this current from their place of growth and carried onward through the lymphatic system.

Transudation and Absorption by Animal Tissues.

If a fresh animal membrane be securely fastened over the lower end of a glass tube, the tube filled with a solution of various substances, and immersed in an exterior vessel of pure water, so that the membrane is a diaphragm, with the water on one side and the solution on the other, it is found that different substances penetrate the membrane and pass through it to the water with different degrees of rapidity. As a rule crystallizable substances, such as mineral salts, glucose, or urea, pass with facility; while non-crystallizable matters, such as albumen, starch, or gum, pass either not at all, or with difficulty. The former are called "diffusible" substances, because they pass through the membrane and become diffused in the water beyond; the latter are "non-diffusible," and do not appear in the exterior liquid, which consequently maintains its purity. This distinction is not absolute, since nearly all soluble substances may be made to transude in some degree by increasing the pressure on the corresponding side of the membrane; but the difference in this respect is often very great.

According to Liebig,* the requisite pressure for different liquids, passing through the same membrane in a given time, is as follows:

PRESSURE REQUIRED TO CAUSE TRANSUDATION THROUGH OX-BLADDER.

Kind of liquid.	Height of the mercurial column.
Water	320 millimetres.
Solution of salt	530 "
Oil	906 "
Alcohol	1280 "

The different diffusibility of different substances has been employed for separating them from each other, when mingled in the same solution. This process is termed *Dialysis.* If a solution containing both gum and sugar be placed on one side of a membranous diaphragm, with pure water on the other, the sugar will pass through, while the gum will be left behind. If a mixture of albumen and sodium chloride be placed under the same conditions, the salt will transude leaving the albumen by itself; the two substances being thus separated by the action of the membrane. By this means poisonous crystallizable matters may be extricated from organic mixtures in sufficient purity for their detection by chemical tests; and on the other hand albuminous matters may be purified from the saline ingredients of the animal fluids, and obtained in a condition for examination and analysis.

Endosmosis and Exosmosis.—Beside the elimination of chemical ingredients, as above described, transudation often gives rise to a change in volume of the fluids on either side of the membrane. When a membrane is interposed between two liquids which are transmitted with different degrees of facility, that which passes most readily will accumulate on the opposite side of the membrane.

If, for example, a solution of salt and an equal volume of distilled water be placed in contact with opposite sides of the membrane, after a time they will have become mingled, to some extent, with each other. A part of the salt will have passed into the water, giving it a saline taste; and a part of the water will have passed into the saline solution, making it more dilute than before. If the quantities of the two liquids be now measured, it will be found that a comparatively large quantity of water has passed into the saline solution, and a comparatively small quantity of the saline solution has passed into the water. That is, the water passes inward to the salt more rapidly than the salt passes outward to the water. The consequence is, that the volume of the saline solution is increased, while that of the water is diminished. The more abundant passage of the water, through the membrane to the salt, is called *endosmosis;* and the more scanty passage of the salt outward to the water is called *exosmosis.*

The mode usually adopted for measuring the rapidity of endosmosis is to take a glass vessel, wide at the bottom and narrow at the top, with a membrane stretched over its larger orifice and secured by a

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* Annales de Chimie et de Physique. Paris, 1849, tome xxv., p. 373.

ligature. To its top there is fitted a narrow upright glass tube, open at both ends. The instrument thus prepared is filled with a saline or organic solution and placed in distilled water; so that the membrane, stretched over its mouth, shall be in contact with water on one side and with the interior solution on the other. As the water then passes in by endosmosis faster than the ingredients of the solution pass out, an accumulation takes place within the vessel, and the fluid rises in the upright tube. The height to which it thus rises in a given time is a measure of the intensity of the endosmosis, and of its excess over exosmosis. Such an instrument is called an *endosmometer*.

Physical Conditions influencing Endosmosis.—The conditions which regulate the rapidity and extent of endosmosis have been investigated by Dutrochet,* Graham, Vierordt, Matteucci, and Cima. The first of these conditions is the *freshness of the animal membrane*. A membrane which has been dried and remoistened, or which has lost its freshness from any cause, will not produce its full effect. If the membrane be allowed to remain and macerate in the fluids, the endosmotic column, after rising to a certain height, begins to descend when putrefaction commences, and the two liquids finally sink to the same level.

The next condition is the *extent of contact* between the membrane and the liquids. The greater this extent, the more rapid is endosmosis. An endosmometer with a wide mouth will produce more effect than with a narrow one, though the volume of liquid may be the same. The action which takes place in the membrane is proportional to its extent of surface.

The *nature of the membrane* employed, and even its *position in regard to the two liquids*, also influence the result. Different membranes act with different degrees of force, since the power of absorption for a given liquid varies with different tissues. In the experiments of Chevreul,† definite quantities of various animal tissues were immersed in different liquids for twenty-four hours; at the end of which time their increase in weight showed the quantity of liquid absorbed. The result is given in the following table:

COMPARATIVE POWER OF ABSORPTION IN DIFFERENT TISSUES.

100 Parts of		Water.	Saline Solution.	Oil.
Cartilage,	absorb in 24 hours,	231 parts.	125 parts.	
Tendon,		178 "	114 "	8.6 parts.
Elastic ligament,		148 "	30 "	7.2 "
Cornea,		461 "	370 "	9.1 "
Cartilaginous ligament,		319 "		3.2 "
Dried fibrine,		301 "	151 "	

Thus the tissue of cartilage will absorb, weight for weight, nearly 30 per cent. more water than that of the tendons; and the cornea will absorb nearly twice as much as cartilage. The animal tissues in general

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* Nouvelles Recherches sur l'Endosmose et l'Exosmose. Paris, 1828.

† In Longet. Traité de Physiologie. Paris, 1861, tome i., p. 383.

absorb water more abundantly than a saline solution; and if a partially dried membrane be placed in a saturated solution of sodium chloride, owing to its rapid absorption of the water, a part of the salt will be left behind and deposited in a crystalline form on its surface.

The position of the membrane exerts a similar influence, owing to a difference of absorbing power in its two surfaces. Matteucci found that, in using the mucous membrane of the ox-bladder with water and a solution of sugar, if the mucous surface of the membrane were in contact with the saccharine solution, the liquid rose in the endosmometer between 80 and 113 millimetres in two hours. But if the same surface were turned toward the water, the rise of the column of fluid was only between 63 and 72 millimetres in the same time.

Another important condition is the *constitution of the two liquids* and their relation to each other. Dutrochet measured the force with which water passes through the mucous membrane of the ox-bladder, into different solutions of similar density, with the following result: *

ENDOSMOSIS OF WATER TOWARD DIFFERENT LIQUIDS.

With solution of	Intensity of endosmosis.
Gelatine	3
Gum	5
Sugar	11
Albumen	12

As a general rule, when the liquids employed are water and a saline solution, the more concentrated the solution, the more active is endosmosis; a larger quantity of water passing toward a denser liquid than toward one which is more dilute. But the above table shows that endosmosis will vary in activity with solutions of different substances, even though they may be of the same density; and when the two liquids used are alcohol and water, endosmosis takes place from the water to the alcohol, that is, from the denser liquid to the lighter.

When two different liquids, therefore, are placed in contact with the membrane, there is usually a comparatively rapid endosmosis in one direction and a comparatively slow exosmosis in the other, according to the rates at which the two liquids traverse the membrane. But in some cases there may be endosmosis without exosmosis. Thus when water and albumen are employed as the two liquids, while the water readily passes inward through the membrane, the albumen does not pass out. If an opening be made in the large end of a fowl's egg, so as to expose the shell-membrane, and the whole immersed in water, endosmosis will take place freely from the water to the albumen, so as to distend the membrane and make it protrude, like a hernia, from the opening in the shell. But the albumen does not pass outward, and the water remains pure. After a time the pressure from within, due to the accumulation of fluid, becomes sufficient to burst the shell-membrane, after which the two liquids mingle with each other.

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* In Matteucci, Physical Phenomena of Living Beings. Pereira's Translation. Philadelphia, 1848, p. 48.

But a substance like albumen, which will not pass out by exosmosis toward pure water, may traverse a membrane which is in contact with a solution of salt. This has been shown with the shell-membrane of the fowl's egg, which, if immersed in a watery solution containing 3 or 4 per cent. of sodium chloride, will allow the escape of a small proportion of albumen. If a mixed solution of albumen and salt be placed in a dialysing apparatus, at first the salt alone will pass outward, leaving the albumen behind; but after the exterior liquid has become perceptibly saline, the albumen also begins to transude in appreciable quantity.

The continuance of endosmosis is favored by *renewal of the two liquids.* Since the accumulation of fluid on one side of the membrane depends on the difference in composition of the liquids employed, when the process has continued for some time, and the two liquids have approximated each other in composition, the activity of endosmosis is diminished in a corresponding degree. But if the exterior liquid be replaced by pure water, and the interior solution maintained at its original strength by the addition of new ingredients, transudation will go on with undiminished activity so long as the membrane retains its absorbent power. The effect of a continuous current in aiding endosmosis may be shown by filling the cleansed intestine of a rabbit with water from a reservoir and then placing it in a shallow vessel containing a dilute solution of hydrochloric acid. If the water be allowed to flow through the intestine under pressure from the reservoir, that which is discharged from its open extremity will in a few seconds show the presence of hydrochloric acid. The acid in this case passes through the coats of the intestine against the pressure of the current, which is of course directed from within outward.

Endosmosis is also regulated, in great measure, by *temperature.* As a rule its activity is increased by moderate warmth. Dutrochet found that an endosmometer, containing a solution of gum, which absorbed only one volume of water at a temperature of 0°, absorbed three volumes at about 34° C. Variations of temperature will sometimes even change the direction of the endosmotic current, particularly with solutions of hydrochloric acid. In the experiments of Dutrochet, when the endosmometer was filled with dilute hydrochloric acid and placed in distilled water at the temperature of 10° C., endosmosis took place from the acid to the water, if the density of the acid solution were less than 1.020; but from the water to the acid, if its density were greater than this. On the other hand, at the temperature of 22° C., the current was from within outward when the density of the solution was below 1.003, and from without inward when it was above that point.

Nature of Endosmosis and Exosmosis.

The continued transudation of a solution through an animal membrane and its diffusion in an exterior fluid are dependent on the simultaneous action of two different properties; first, the absorbent capacity of the membrane for the solution, and secondly, the capacity of the solution for diffusing itself in the exterior fluid. The simplest illustration of the process is that of the transudation and evaporation of moisture. If a fresh animal membrane be exposed to the air under ordinary circumstances, it at once begins to lose water by evaporation; and the loss will continue, under favorable hygrometric conditions, until the whole of the water has disappeared in the atmosphere and the membrane is completely desiccated. But if the membrane be placed with its upper surface in contact with the air, and its lower surface in contact with water or a watery fluid, it no sooner loses a portion of its water by evaporation than it absorbs a corresponding quantity from beneath. There is thus a continual passage of water from the fluid, through the membrane, to the atmosphere, until the whole of it has been exhausted; the membrane retaining its own proportion of moisture, while losing water by one surface and absorbing it by the other.

A similar interchange will take place if one surface of the membrane is in contact with water and the other with a saline or saccharine solution; provided the solution be sufficiently concentrated to absorb water from the membrane. Each layer of the membrane absorbs from that next to it sufficient moisture to replace that which has passed into the solution; and endosmosis thus goes on from the water to the solution through the animal membrane.

In this instance, however, there will be a double action. As the membrane has an absorptive power for both the water and the ingredients of the solution, and as these two are diffusible in each other, they will both be transferred in opposite directions. But since the membrane absorbs water more readily than the ingredients of the solution, it can supply these ingredients to the water on one side less abundantly than it can supply water to the solution on the other. Consequently a larger volume of water passes to the solution than *vice versâ*, and endosmosis preponderates over exosmosis.

It is evident accordingly that, whatever be the relation of the two liquids to each other, the first requisite for their transudation is the absorptive power of the animal membrane. A membrane in contact with two different liquids will nearly always absorb one of them more rapidly than the other; and if in contact with a solution containing several ingredients, it will take up some of these ingredients in greater, others in smaller proportion. A substance, therefore, which the intervening membrane does not absorb at all, cannot be transferred to the fluid beyond it. The membrane acts as a barrier to exclude ingredients for which it has no absorptive power, but is ready to supply those which it can take up with facility.

An equally important condition of endosmosis and exosmosis is the diffusibility of different liquids in each other. This subject was investigated by Graham* in the following manner: Glass vessels, filled

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* Annalen der Chemie und Pharmacie. Heidelberg, 1851. Band lxxvii., p. 56.

with various saline solutions, were immersed in reservoirs of pure water, so that the level of the water in the reservoir was a little higher than that of the solution in the interior vessel; and after they had been allowed to remain for a time at rest, at a constant temperature, the quantity of solution which had escaped into the surrounding liquid indicated the rapidity with which diffusion had taken place. By this method it was found that the diffusibility of different liquids varies in an analogous way with their absorption by animal tissues, and is influenced by similar conditions. Solutions of different salts, in the same degree of concentration, are diffused with different degrees of rapidity; and the same solution, other conditions remaining equal, increases in diffusibility with the elevation of temperature. The following table shows the comparative diffusibility of various saline solutions in pure water at different temperatures:

DIFFUSIBILITY OF SALINE SOLUTIONS IN PURE WATER.

	At 3° C.	At 15.3° C.
Sodium chloride	22.47	32.25
Sodium nitrate	22.79	30.70
Ammonium chloride	31.14	40.20
Potassium nitrate	28.70	35.55
Potassium iodide	28.10	37.00
Magnesium sulphate	13.07	15.45

The rapidity of diffusion is influenced, not only by temperature, but also by the degree of concentration of the solution and by the chemical constitution of the salt which it contains. A concentrated solution diffuses into pure water more rapidly than one which is comparatively dilute; and if the solution be maintained at its original degree of concentration while the exterior liquid is replaced by pure water, diffusion continues with greater energy than if the two liquids are allowed to become changed by mutual admixture. Salts of potassium diffuse more rapidly than the corresponding salts of sodium; and in each instance salts of the monobasic acids diffuse more rapidly than those of bibasic acids with the same metals. Sugar, gum, and albumen are less diffusible than the soluble mineral salts, and of all the substances examined albumen is the least so, being diffused only one-twentieth part as readily as sodium chloride. Urea, on the other hand, is nearly as diffusible as sodium chloride If the interior vessel contain a mixed solution of several substances, each is diffused with its own specific rapidity, so that after a time they are found in the water of the reservoir in different quantities. Various other peculiarities are observed, showing the influence of the chemical character of a salt upon its diffusibility.

In the experiments of Hoppe-Seyler,* the influence of repose or agitation on the rate of diffusion was fully demonstrated. Concentrated solutions of sugar, albumen, or other substances having a rotatory

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* Physiologische Chemie. Berlin, 1877, p. 145.

action on polarized light, were placed at the bottom of a glass vessel, the remainder of which was filled with pure water. The quantity of the substance in solution at any level above or below the plane of contact of the two liquids could then be determined by means of a saccharimeter; and the examination could be repeated at will without disturbing the apparatus. It was found that, under these conditions, diffusion took place with readiness only in the immediate vicinity of the contact of the two liquids. Solutions of gum or albumen after several days, had mingled with the water only for a height of one or two centimetres above and below the plane of contact; and with a concentrated solution of cane sugar, at the end of four weeks the layer of diffusion was only 15 centimetres in thickness. But any mechanical shock or disturbance hastens the process of diffusion and admixture; and with solutions of gum, sugar, or albumen, a few seconds' agitation may produce a uniform mixture which would require an indefinite time by diffusion in a state of rest.

Absorption and Transudation in the Living Body.

All the conditions favorable to endosmosis and exosmosis, shown by the above experiments, are present in the living body. The organic tissues and membranes have their normal constitution maintained by the process of nutrition, and exert their special absorptive power on each ingredient of the animal fluids. The extent of absorbing surface is multiplied by the subdivision of the blood-vessels, the glandular tubes, and the anatomical elements of the organs. The fluids are in immediate contact with the absorbing surfaces, at a nearly uniform, moderately elevated temperature; and the movement of the blood and lymph supplies the requisite ingredients by constant renewal, and incessantly removes the surplus of transuded material.

In the living body, accordingly, transudation takes place with great rapidity. It has been shown by Gosselin, that if a watery solution of potassium iodide be dropped on the cornea of a rabbit, the iodine passes into the cornea, aqueous humor, iris, lens, sclerotic and vitreous body, in the course of eleven minutes; and that it will penetrate the aqueous humor in three minutes, and the substance of the cornea in a minute and a half. In these experiments it is evident that the iodine passes into the deeper portions of the eye by endosmosis, and not by transportation through the blood-vessels; since it is not found in the tissues of the opposite eye, examined at the same time.

The same observer has shown that the active principle of belladonna penetrates the tissues of the eyeball in a similar manner. He applied a solution of atropine sulphate to both eyes of two rabbits, and in half an hour the pupils were dilated. Three-quarters of an hour later, the aqueous humor was collected by puncturing the cornea with a trocar; and this fluid, dropped on the eye of a cat, produced dilatation and immobility of the pupil in half an hour. The aqueous humor of the affected eye consequently contains atropine, which has been absorbed through the cornea, and acts directly on the muscular fibres of the iris.

But in all vascular organs, endosmosis and exosmosis are further accelerated by the movement of the blood.

If a solution of nux vomica be injected into the subcutaneous connective tissue of the hind leg of two rabbits, in one of which the local circulation is unimpeded, while in the other it has been arrested by ligature of the blood-vessels of the limb, in the first animal the poison will be absorbed with sufficient rapidity to produce its specific effects in a few minutes; but in the second, absorption will be retarded, and the poison will find its way into the general circulation so slowly, that its action will be manifested only at a late period, or even not at all.

Albumen, under ordinary conditions, is but very slightly endosmotic or diffusible; while peptone possesses these properties in a marked degree. Peptone, accordingly, after its production by the digestive process, is readily absorbed from the intestine and enters the blood-vessels; but the albumen of the blood, in the normal state of the circulation, is not exuded from the secreting surfaces. If the pressure, however, within the capillary vessels be increased by venous obstruction, not only the saline and watery parts of the blood pass out in larger quantities, but the albumen also transudes and infiltrates the neighboring parts. In this way albumen may make its appearance in the urine, from disturbance of the renal circulation; and local œdema or general anasarca may follow upon venous congestion in particular regions or at the centre of the circulation.

The Lymph and Chyle.

The lymph is the fluid which, having been absorbed from the various tissues and organs of the body, is transported by the lymphatic vessels and discharged into the great veins near the heart. As the chyle is simply the fluid of the mesenteric lymphatics, which has become white and opaque, from the absorption of digested fat, it is properly studied at the same time with the lymph in general. Lymph may be obtained from the living animal by introducing a canula into the thoracic duct at the root of the neck, or into the lymphatic trunks in other regions. It was collected by Rees from the lacteals of the mesentery and from the lymphatics of the leg in the ass, by Colin from the lacteals and thoracic duct of the ox, and from the lymphatics of the neck in the horse. We have obtained it from the thoracic duct in both the dog and the goat.

Physical Characters and Composition of Lymph.—The lymph, as obtained from the thoracic duct in the intervals of digestion, is an opalescent or nearly transparent, alkaline fluid, usually of a light amber color, and having a specific gravity of 1022. Its analysis shows a close resemblance in composition with the plasma of the blood. It contains water, fibrinogen, albumen, fatty matters, and the usual saline substances of the animal fluids. It is, however, poorer in albuminous ingredients than the blood. The following is an analysis, by Lassaigne,* of the fluid obtained from the thoracic duct of the cow:

Composition of the Lymph.

Water	964.0
Fibrine	0.9
Albumen	28.0
Fat	0.4
Sodium chloride	5.0
Sodium carbonate Sodium phosphate Sodium sulphate	1.2
Lime phosphate	0.5
	1000.0

Owing to the presence of fibrinogen, the lymph coagulates like blood, within a few moments after its removal from the lymphatic vessels, forming a gelatinous mass, more or less colorless and transparent, or whitish and opaque, according to the proportion of fatty matter present. After coagulation, it separates into a liquid serum and a solid clot.

In lymph from the thoracic duct, the clot, within a few moments after coagulation, usually assumes a pinkish color, and on microscopic examination is found to contain a few red blood-globules. Their presence is attributed by some observers (Kölliker, Robin) to the accidental rupture of capillary blood-vessels and consequent introduction of their contents into the lymphatic system; but their occurrence is so constant that it must be doubted whether they are altogether of accidental origin. The pinkish color is never perceptible in lymph when first drawn from the vessels, but only after it has been a short time exposed to the air.

The fluid drawn from the thoracic duct, especially in carnivorous animals, varies, both in appearance and constitution, at different times. In the ruminating and graminivorous animals, as the sheep, ox, goat, and horse, it is either opalescent, with a slight amber tinge, or nearly transparent and colorless. In the dog and cat, it is also opaline and amber colored in the intervals of digestion, but soon after feeding becomes of a dense, milky white, and continues to present that appearance until digestion and absorption are complete. It then regains its original aspect, and remains opaline until digestion is again in progress.

This variation is due to the absorption of fatty matters during digestion. The chyle is richer than lymph in nearly all its solid ingredients, but the principal difference between the two consists in the proportion of fat, which is nearly absent from the transparent or opaline lymph, but abundant in the white and opaque chyle. This is shown in the following analysis, by Rees,† of lymph and chyle,

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* In Colin, Physiologie comparée des Animaux domestiques. Paris, 1856, tome ii., p. 111.

† London Medical Gazette. London, 1841, vol. i., p. 547.

taken respectively from the lacteals of the abdomen and the lymphatics of the hind leg, in the ass.

COMPARATIVE ANALYSIS OF LYMPH AND CHYLE.

	Lymph.	Chyle.
Water	965.36	902.37
Albumen	12.00	35.16
Fibrine	1.20	3.70
Spirit extract	2.40	3.32
Water extract	13.19	12.33
Fat	traces	36.01
Saline matter	5.85	7.11
	1000.00	1000.00

When a canula, accordingly, is introduced into the thoracic duct at different periods after feeding, the fluid discharged varies considerably, both in appearance and quantity. In the dog, it is never quite transparent, but retains a marked opaline tinge even so late as eighteen hours after feeding on lean meat, and at least three days and a half after the introduction of fat food. Soon after feeding, it becomes whitish and opaque, and so remains during the continuance of digestion and absorption. After this it resumes its former appearance, becoming light colored and opalescent in the carnivorous animals, and nearly transparent in the herbivora.

The Lymph Globules.—The lymph nearly always contains rounded, transparent, or finely granular nucleated cells, from 6 to 12 mmm. in diameter, similar in appearance to the white globules of the blood, and known as "lymph-globules." According to Kölliker they vary much, both in number and size, according to the part of the lymphatic system from which the fluid is taken. In the smallest lymphatic vessels of the mesentery, they are scanty or altogether absent; and in the lymphatics, where they first show themselves, they are few in number and of small size. But after the lymph has traversed one or two ranges of lymphatic glands, the globules are more numerous and larger, often attaining the size of 12 mmm. in diameter. From this circumstance, as well as from the microscopic texture of the lymphatic glands, it is concluded that the lymph-globules originate, in great part, in the interior of the glands, and that they are brought thence by the current traversing the lymph-paths in the substance of these organs.

Movement of the Lymph in the Lymphatic Vessels.—The movement of the fluid in the lymphatic system differs from that of the blood, in the important particular that its course is always in one direction, namely, from the periphery toward the centre. It is absorbed by the lymphatic capillaries, collected into the lymphatic branches and trunks, and thence conducted to the great veins near the right side of the heart.

The cause of this centripetal movement of the lymph is primarily the *force of endosmosis* acting at the confines of the lymphatic system. As the volume of fluid accumulates in an endosmometer, the ingredients of the lymph penetrate by absorption into the lymphatic capillaries, and thence into the larger vessels of the system. It is evident that the pressure of a fluid from endosmotic action may be very considerable, since it can sustain a column of mercury at the height of 600 millimetres, and may burst the shell membrane of a fowl's egg placed in contact with water. As this pressure, in the lymphatic system, is always from without inward, and as the main lymphatic trunks terminate in the veins, the result is a uniform movement of the lymph, from the peripheral parts toward the centre of the circulation.

As the lymphatic vessels, like the veins, are provided with valves, opening toward the centre and closing toward the periphery, the contraction and relaxation of the voluntary muscles in the limbs and trunk must facilitate the passage of the fluids in an inward direction. The pulsations of the heart and aorta also contribute to this result. As the thoracic duct passes obliquely through the chest, between the spinal column and the aorta, at each aortic pulsation it is compressed, and its contents propelled upward. This effect is often visible in the experiment of collecting lymph from the thoracic duct at the root of the neck; the lymph being often projected from the extremity of the canula in a distinct jet at each cardiac pulsation.

Lastly, the respiratory movements of the chest take part in maintaining the flow of lymph. At each inspiration the resistance in the thorax is diminished, and the lymph passes more readily from below into the thoracic duct; at each expiration the duct is subjected to compression and thus emptied toward the veins. When artificial respiration is kept up through the trachea after the chest has been opened, the influence of the respiratory movement is reversed. The flow of lymph from the thoracic duct is then perceptibly increased at each insufflation of the lung, since this produces a momentary pressure within the chest.

Of the forces above enumerated for the production of the lymph-current, the most important and continuous is endosmotic action. The remainder are more or less irregular or intermittent, but they contribute by mechanical aids to the same result; and the effect of the whole is an incessant transportation of the lymph from the periphery to the centre, where it is mingled with the returning current of venous blood.

Daily Quantity of the Lymph and Chyle.—The quantity of fluid passing through the thoracic duct varies according to the condition of abstinence or digestion. In the fasting condition it is comparatively moderate, but becomes more abundant soon after the commencement of digestion, to diminish again during its later stages. We have found, at various periods after feeding, in the dog, the following quantities discharged from the thoracic duct per hour, for every thousand parts of bodily weight:

HOURLY QUANTITIES OF LYMPH AND CHYLE IN THE DOG, PER THOUSAND PARTS OF BODILY WEIGHT.

3½ hours after feeding	2.45
7 " " "	2.20
13 " " "	0.99
18 " " "	1.15
18½ " " "	1.99

It would thus appear that the hourly quantity of these fluids, after increasing with digestion and diminishing during its latter stages, again increases somewhat about the eighteenth hour. It is probable that this double increase is owing to two causes. The fluid obtained in greatest abundance in the dog, from 3 to 7 hours after feeding, is white and very opaque, and its quantity is largely due to the admixture of chyle absorbed from the intestine. That drawn about the eighteenth hour is opaline, or nearly transparent, and consists of lymph alone. The absorption of chyle, therefore, takes place while digestion is in progress; but the production of lymph occurs most abundantly some hours later, after the materials of nutrition have reached and permeated the tissues.

The daily quantity of lymph and chyle has been found, by direct observation, much larger than would be anticipated. In two experiments on the horse, extending over a period of twelve hours each, Colin * obtained from the thoracic duct, on the average, 893 grammes of fluid per hour, which, if continued for the remaining twelve hours, would amount to rather more than 20 kilogrammes per day. In the ruminating animals, according to the same observer, the quantity is still greater. In a cow of ordinary size, the smallest amount obtained, in an experiment extending over twelve hours, was 625 grammes in fifteen minutes; that is, 2500 grammes per hour, or 60 kilogrammes per day. In another experiment with a young bull weighing 185 kilogrammes, he withdrew from the thoracic duct in twenty-four hours, 15 kilogrammes of lymph and chyle, representing a little more than 8 per cent. of the entire bodily weight.

We have obtained similar results in the dog and the goat. In a young kid weighing 6.36 kilogrammes, 122.5 grammes of lymph were collected from the thoracic duct in three hours and a half. This represents 35 grammes per hour, and, if continued throughout the day, would amount to 640 grammes, or fully 10 per cent. of the bodily weight. In the dog the fluids from the thoracic duct were less abundant; the total daily quantity in this animal, according to the average of observations at various periods after feeding, being very nearly four and a half per cent. of the bodily weight. This is substan-

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* Physiologie comparée des Animaux domestiques. Paris, 1856, tome ii., p. 106.

tially the same result as that obtained by Colin in the horse; and for a man weighing 65 kilogrammes, it would be equivalent to about 3000 grammes of lymph and chyle per day. This represents both the products of lymphatic transudation and those of intestinal absorption. An estimate of the lymph alone must be based upon the quantity of fluids passing through the thoracic duct in the intervals of digestion, when no chyle is absorbed from the intestine. In the dog, the average quantity obtained, from the thirteenth to the nineteenth hour after feeding, was about 1.30 per thousand parts of the bodily weight; or, for the whole twenty-four hours, a little over 3 per cent. of the bodily weight. For a man of medium size, this would give not far from 2000 grammes as the average daily quantity of lymph alone.

Internal Renovation of the Animal Fluids.—The combined operation of secretion, transudation, and reabsorption produces a continual interchange of the animal fluids, which is dependent for its materials upon the blood, and which may be considered as a kind of secondary circulation through the substance of the tissues. All the fluids discharged into the small intestine are reabsorbed and again enter the current of the circulation. They pass and repass through the mucous membrane of the alimentary canal and adjacent glands, becoming more or less altered, but still serving to renovate alternately the blood and the secretions. The elements of the blood transude in part from the capillary vessels, and are taken up from the tissues by the lymphatics, to be again restored to the circulation at its venous extremity.

The quantity of fluids thus transuded and reabsorbed will serve to indicate the activity of endosmosis and exosmosis in the living body. In the following table, the amounts are estimated, from the preceding data, for a man of average size:

FLUIDS TRANSUDED AND REABSORBED DURING TWENTY-FOUR HOURS.

Saliva	1280	grammes.
Gastric juice	3000	"
Pancreatic juice	800	"
Bile	1000	"
Lymph	2000	"
	8080	"

Not less than 8000 grammes therefore of the animal fluids, a quantity equal to that of the entire blood and amounting to more than 12 per cent. of the bodily weight, transude through the membranes and are restored to the blood by reabsorption, in the course of a day. By this process the natural constitution of the parts, though constantly changing, is maintained in its normal condition, through the movement and renovation of the circulating fluids.

CHAPTER VIII.

THE URINE.

THE urine is distinguished from other animal fluids by the fact that it represents the product of physiological disintegration. The various manifestations of force in the living body, such as heat, sensibility, and motion, are produced at the expense of its materials, by their metamorphosis in the process of nutrition. The transformation and renewal of its constituents are accordingly essential conditions of its vital activity. Every living being absorbs from without nutritive materials, which are modified by assimilation and converted into the ingredients of its tissues; and at the same time its elements pass into new forms of combination, to be expelled as the products of disintegration.

Certain substances, therefore, are constantly making their appearance in the body, which were not introduced with the food, but which have been produced by retrograde metamorphosis. They are derived from materials which once formed part of the animal tissues, but which have become altered by internal transformation, and are no longer capable of aiding in the performance of the functions. The elimination and removal of these materials is the process of *excretion*, and the materials themselves are known as *excrementitious substances.*

The excrementitious substances are formed for the most part in the tissues, from which they are absorbed by the blood and conveyed to excretory organs by which they are discharged. If their elimination be impeded, their accumulation in the system produces a disturbance, which is more or less severe according to their special character and the rapidity of their production. This disturbing influence is especially manifested in its action upon the nervous system, causing abnormal irritability, derangement of the senses, and, in extreme cases, delirium, insensibility, and death.

In the normal condition and in normal quantities, the excrementitious matters are not poisonous, nor even deleterious; they are the natural products of functional activity, and therefore as essential to the manifestation of life as the nutritious material supplied by the food. It is only when their elimination is retarded that they interfere with the performance of the functions, by deranging the constitution of the tissues.

Some of the excrementitious matters produced in the body are probably eliminated, in small proportion, with the perspiration or the feces; and carbonic acid is abundantly exhaled from the lungs. But among the most important of these substances are those which contain nitrogen. This element indicates their derivation from the albumenoid ingredients of the body, and they present in other respects a mutual analogy in chemical properties and composition. They accordingly form a group of organic substances, resembling each other in origin, constitution, and physiological destination. They are eliminated from the body by the urine, of which they form the characteristic ingredients.

The urine is therefore solely an excretion. It is a solution of the nitrogenous excrementitious matters of the body; and by its abundance and composition it indicates the activity of metamorphosis in the nitrogenous ingredients of the tissues and fluids. It also contains most of the mineral salts discharged from the body; and by the water which holds these matters in solution it represents a large proportion of the fluids passing through the system. Furthermore, accidental or abnormal ingredients, introduced into the blood, are usually eliminated by this channel, and appear as temporary ingredients of the urine. The constitution and variations of the urine during health, and its alteration in disease, are regulated by the corresponding changes of nutrition in the body at large. It is therefore one of the most essential products of the animal system, and its formation is second in importance only to the function of respiration.

Physical Properties of the Urine.

The urine is a clear, amber-colored fluid, of a watery consistency and distinctly acid reaction. It is usually so nearly transparent, that no turbidity is perceptible by ordinary diffused light. It contains, however, a small quantity of mucus from the urinary bladder, which becomes visible as a faint opalescence when a sunbeam is made to pass through it in a lateral direction. After remaining for some hours at rest in a cylindrical vessel, the mucus subsides, forming a light cloud at the bottom and leaving the supernatant fluid clear. The average specific gravity of healthy urine, in the adult, is from 1020 to 1025; and its daily quantity about 1200 cubic centimetres.

Variations in Quantity, Acidity, and Specific Gravity.—The urine is habitually discharged from the bladder five or six times in the twenty-four hours, each specimen showing more or less variation in its physical properties. This depends on the changing conditions of the body, as to rest, exercise, food, drink, sleep, and wakefulness. In the same person, leading a uniform mode of life, the diurnal variations of the urine follow each other with considerable regularity; though they may not be altogether the same in different individuals. As a rule, the urine which collects during the night and is first discharged in the morning is strongly colored, of high specific gravity, with a very distinct acid reaction. During the forenoon it is pale and of diminished density; its specific gravity often falling so low as 1018 or 1015. At the same time, its acidity diminishes or disappears; so that it may be either faintly acid, neutral, or slightly alkaline. Its density and depth of color then increase, and its acidity returns; all these properties becoming more strongly marked during the afternoon and evening. Toward night it is again deeply colored and strongly acid, and its specific gravity often 1028 or 1030.

These variations are liable to modification from temporary causes. The color, acidity, and specific gravity of the urine may be diminished at any time by large draughts of liquid or the use of diuretic mineral waters; or they may be increased by abstinence from drink or by copious perspiration. Its acidity is also liable to vary from the use of food, such as summer fruits or vegetables, containing salts of the organic acids, namely, lactates, acetates, malates, and tartrates. These salts, when introduced into the system, are replaced by carbonates of the same bases and appear under that form in the urine, reducing for the time its acidity, or even causing its alkalescence.

It is evident, therefore, that when the specific gravity and acidity of the urine are to be tested, it will not be sufficient to rely upon the examination of a single specimen. Its normal variation in specific gravity may reach the limits of 1015 as a minimum and 1030 as a maximum; but either of these would be unnatural if continued for twenty-four hours. All the specimens of urine passed during the day should therefore be collected and examined together. The mean specific gravity thus obtained will represent its normal daily density.

Its daily volume is also to be taken into account. The total amount of solids discharged by the urine in health is from 50 to 60 grammes per day; and this quantity is dissolved in about 1200 cubic centimetres of water. This gives an average daily quantity and an average specific gravity of the urine, as the measure of the excretory process during twenty-four hours.

Both the quantity of the urine and its mean specific gravity are liable to vary in the same individual from day to day; but when this is due to physiological or temporary causes, the variations of quantity and specific gravity are in inverse ratio to each other. Usually the water of the urine is more than sufficient to hold all its solid matters in solution; and its proportion may therefore be lessened without the production of turbidity or the formation of a deposit, the urine merely becoming deeper in color, and of higher specific gravity. If the quantity of drink be diminished, or if the exhalation from the lungs and skin, or the intestinal discharges, be increased, a smaller quantity of water will pass off by the kidneys; and the urine will be diminished in quantity, while its specific gravity is increased. The urine is sometimes reduced in this way to 500 or 600 cubic centimetres per day, its mean specific gravity rising at the same time to 1030. On the other hand, if the fluid ingesta be unusually abundant, or if the perspiration be diminished, the surplus water will pass off by the kidneys; the amount of urine in twenty-four hours being increased to 1500 or 1600 cubic centimetres, and its mean specific gravity reduced to 1020 or 1015. These changes depend simply on the fluctuating quantity of water in the urine; its total amount of solid matter remaining about the same. If, however, both its quantity and mean specific gravity be increased or diminished at the same time, or if either one be increased or diminished while the other remains stationary, this would show an actual change in the amount of solid ingredients, and consequently an abnormal condition.

Ingredients of the Urine.

The chemical composition of the urine, as derived from numerous analyses, is as follows:

Composition of the Urine.

	Water	950.00
Nitrogenous organic substances.	Urea	26.20
	Creatinine	0.87
	Sodium and potassium urates	1.45
	Sodium and potassium hippurates	0.70
Mineral salts.	Sodium biphosphate	0.40
	Sodium and potassium phosphates	3.35
	Lime and magnesium phosphates	0.83
	Sodium and potassium chlorides	12.55
	Sodium and potassium sulphates	3.30
	Mucus and coloring matter	0.35
		1000.00

Urea.—This is the most important constituent of the urine, both in character and amount, forming more than one-half its solid ingredients, and over 80 per cent. of all those of an organic nature. The most important fact known with regard to the origin of urea is, that it is not formed in the kidneys, but pre-exists in the blood and is drained away from the circulating fluid during its passage through the renal vessels. It has been found in the blood of the human subject in cases of renal disease, in so large a proportion as 1.5 parts per thousand,* or nearly ten times its normal quantity.

Urea is most readily obtained from urine by first converting it into a nitrate. For this purpose the fresh urine is evaporated over the water-bath to one-quarter of its original volume. It is then filtered, and the filtered fluid mixed with an equal quantity of nitric acid. The nitrate of urea thus produced, being less soluble than urea, is deposited in abundant crystalline scales. The deposit is separated by filtration from the mother liquor, mixed with water, and decomposed by the addition of barium carbonate, which sets free the urea, with the formation of barium nitrate. This process is continued so long as carbonic acid is given off; after which the whole is evaporated to dryness, and the dry residue extracted with absolute alcohol, which dissolves the

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* In Milne Edwards, Leçons sur la Physiologie. Paris, 1857, tome i., p. 298.

urea. The alcoholic solution is then filtered and evaporated until the urea separates in a crystalline form.*

The quantity of urea in a given volume of urine is ascertained by decomposing it, according to Davy's method, with a solution of sodium hypochlorite. A narrow graduated glass tube, open at one extremity, with a capacity of about 50 cubic centimetres, is filled to a little more than one-third its height with mercury, upon which are poured 3 or 4 cubic centimetres of the urine to be examined. The remainder of the tube is then filled with the sodium hypochlorite solution, its mouth closed, the fluids well mixed by agitation, and the tube inverted in a shallow dish filled with a saturated solution of sodium chloride. The mixture of urine and hypochlorite solution remains in the tube; and as the urea is decomposed, its nitrogen collects in the upper end of the tube, where its volume may be read off on the scale, after the action has ceased. Every cubic centimetre of nitrogen, thus disengaged, represents 2.5 milligrammes of urea.

The results obtained by nearly all experimenters led to the conclusion that the quantity of urea excreted is especially increased by *muscular exertion*, until a doubt was thrown on this point by Fick and Wislicenus in 1866. These observers ascended a mountain on foot, the ascent occupying a little over eight hours; during which time, and for seventeen hours beforehand, they confined themselves to a diet of non-nitrogenous food. They found the hourly amount of urea discharged less during the ascent than it was before; but it increased during the following night, after a meal of animal food.

Subsequent observers have obtained various results. Parkes,† in a series of extended observations, found that the discharge of urea was increased not during, but after, a period of muscular work. This was shown even in a man confined for five days to a non-nitrogenous diet, in whom the discharge of urea was not increased on the day of unusual muscular effort, but on the following day was a little more than doubled.

The observations of Flint,‡ in the case of the pedestrian Weston, have the advantage of extending over comparatively long periods, both of exercise and rest, the diet remaining unchanged in general character.

The pedestrian was under observation for fifteen days; namely, five days previous to the walk, five days during its continuance, and five days immediately afterward. For the period preceding the walk, the average exercise was about eight miles per day; during the walk it was nearly sixty-four miles per day, and for the subsequent period a little over two miles per day. The results obtained represent accordingly the amount of urea excreted under ordinary conditions, that discharged during unusual muscular exertion, and the subsequent effects of the exertion on the general system.

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* Hoppe-Seyler, Handbuch der Physiologisch- und Pathologisch-Chemischen Analyse. Berlin, 1870, p. 120.

† Proceedings of the Royal Society of London, vol. xvi., p. 48, and March 2, 1871.

‡ New York Medical Journal, June, 1871.

The nitrogenous ingredients of the food, during all three periods, were also recorded, so that their influence could be estimated at the same time with that of the muscular exertion.

The following table gives the main result of these experiments, as connected with the present subject:

Daily Quantity of	First Period. Five days before the walk.	Second Period. Five days during the walk.	Third Period. Five days after the walk.
Urea	628.24 grains.	722.16 grains.	726.79 grains.
Nitrogen in food . . .	339.46 "	234.76 "	440.93 "
Nitrogen in urea . . .	293.18 "	337.01 "	339.17 "
Total nitrogen in urea and feces	315.09 "	361.52 "	373.15 "
Nitrogen in urea and feces per 100 parts of nitrogen in food	92.82	153.99	84.63

It is evident, therefore, that during unusual muscular exertion the daily quantity of urea was increased by nearly fifteen per cent., the nitrogenous elements of the food being at the same time diminished; and that the total quantity of nitrogen discharged by the urea and feces combined was more than fifty per cent. greater than that introduced with the food, while in both the previous and subsequent periods it was from seven to fifteen per cent. less. Five years later, observations were made on the same pedestrian by Pavy,* during a six days' walk, averaging 75 miles per day, with similar results; there being an increased discharge of urea, and an increased elimination of nitrogen not accounted for by that taken with the food.

Creatinine.—This substance is closely allied to urea in chemical composition, but is produced in much smaller quantity; its total amount not usually exceeding 1 gramme per day. It is probably, like urea, a final product of the metamorphosis of albumenoid matters, but it is no doubt immediately derived from the creatine of muscular tissue, from which it may be artificially produced by the action of heat and dilute sulphuric acid. But little is known with regard to the conditions which increase or diminish its production in the body.

Sodium and Potassium Urates.—The uric acid of the sodium and potassium urates is a nitrogenous organic acid, belonging to the class of excrementitious matters. Like urea, it is increased in quantity by a nitrogenous, and decreased by a non-nitrogenous diet; but its relations to muscular exercise and other temporary conditions are not fully known. The urates are readily soluble in water, and are usually excreted to the amount of about 1.75 gramme per day. The *hippurates* are similar in their general physiological relations to the urates, excepting that they are more abundant under a vegetable diet, and disappear altogether under the exclusive use of animal food. In man, under an ordinary mixed diet, they are about one-half as abundant as the urates.

Sodium Biphosphate.—This is the ingredient which gives to the

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* London Lancet, 1876. Vol. ii., p. 848.

urine its acid reaction. It is regarded as derived from the sodium phosphate of the blood ($Na_2H PO_4$) by the action of uric acid, which unites with a part of its sodium, forming sodium urate, and leaving an acid sodium phosphate (NaH_2PO_4). The uric acid produced in the system, though not eliminated in a free form, causes, therefore, indirectly the acid reaction of the urine; and this reaction will vary in intensity with the amount of its production.

The Alkaline Phosphates, or phosphates of sodium and potassium.—These phosphates exist in the blood as well as in the urine, and in solution have a mildly alkaline reaction. Owing to their ready solubility, they never appear as a precipitate, nor disturb in any way the transparency of the urine. It is as a constituent of these salts that most of the phosphoric acid in combination is discharged with the urine. According to Vogel, its excretion is increased by food containing soluble phosphates or substances capable of yielding phosphoric acid in the system. It is accordingly more abundant under a diet of animal food, less so under a vegetable regimen. It is not, however, exclusively derived from the food, since it is still discharged, though in diminished quantity, after long-continued abstinence. Its immediate origin is, therefore, wholly or partly from the constituents of the body itself. The observations of Wood,* as well as those of Vogel, show a diurnal variation of considerable regularity in the excretion of the phosphatic salts. It is at a minimum during the forenoon, increases in the latter part of the day after the principal meal, and reaches a maximum in the evening or during the night, to diminish again on the morning of the following day. The average quantity of the alkaline phosphates discharged under an ordinary diet is a little over four grammes per day.

The Earthy Phosphates, or phosphates of lime and magnesia.—The earthy phosphates are usually excreted in much smaller quantity than the preceding. They are held in solution by the acid reaction of the urine, and when this reaction is absent or much diminished they are thrown down as a light precipitate. The neutral or faintly alkaline urine, often passed in the forenoon, may therefore be turbid with a deposit of earthy phosphates, without indicating any abnormal increase in their amount. According to the observations of Wood, the alkaline and earthy phosphates differ in the conditions influencing their excretion. During continued mental application, the alkaline phosphates are increased, while the earthy phosphates are diminished; the amount of both combined being not materially altered. The average daily quantity of the earthy phosphates is about one gramme, or rather less than one-quarter that of the alkaline phosphates.

Sodium and Potassium Chlorides.—Sodium chloride, which represents nearly the whole of these salts, is by far the most abundant mineral ingredient in the urine, forming over one-half of its inorganic constituents. It is mainly derived from the food, and is increased

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* Proceedings of the Connecticut Medical Society, 1869.

or diminished according to its amount in various articles of diet. Its discharge is usually least during the night, increases in the forenoon, and is greatest during the latter part of the day. According to Vogel,* both mental and bodily exertion perceptibly augment its excretion; and even water, when taken in unusual quantity, by increasing the activity of the kidneys, causes a more abundant discharge of sodium chloride, subsequently followed by a corresponding diminution. The average amount of chlorides eliminated with the urine is about fifteen grammes per day.

Sodium and Potassium Sulphates.—The sulphates in the urine are derived partly from those introduced with the food. Their quantity is increased by the administration of sulphuric acid or of sodium sulphate; and the administration of sulphur or a sulphuret produces the same effect. They are most abundant under a diet of animal food, owing to the sulphur contained in albuminous matters, which is finally eliminated in the form of sulphates. These salts are freely soluble and never appear as a precipitate in the urine. Their average quantity is about 3.96 grammes per day.

Reactions of the Urine to Chemical Tests.

The reactions of the urine to various ordinary tests form a ready criterion for ascertaining its normal or abnormal constitution. The exact quantitative determination of its ingredients requires the skill of the professional chemist; but many of its important characters may be recognized by simple means.

Application of Heat.—If healthy urine, of a distinctly acid reaction, be heated to the boiling point, no change in its appearance is produced; but if its acidity be very slight, it may become turbid on boiling, from a precipitation of earthy phosphates. These phosphates are less soluble in a hot than in a cold liquid; and a faintly acid reaction, which may hold them in solution at ordinary temperatures, becomes insufficient under the application of heat, and the phosphates are precipitated. The deposit from this cause is never very abundant, and is at once redissolved by the addition of any acid sufficient to restore the normal reaction of the urine. The precipitation of the earthy phosphates by boiling is, therefore, due, not to an increased quantity of these salts, but to deficient acidity of the urine.

Diseased urine may become turbid on boiling, from the coagulation of *albumen.* This is distinguished from a precipitation of the earthy phosphates by two facts—namely, first, that it may take place in urine which is distinctly acid; and second, that the addition of nitric acid, which redissolves the phosphatic precipitate, only increases the turbidity due to albumen.

Acids.—The addition of mineral acids to healthy urine produces no immediate visible effect, beyond increasing its acidity and slightly modi-

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* Analyse des Harns. Wiesbaden, 1872, p. 350.

fying its color. They, however, decompose its urates; and the uric acid thus set free is slowly deposited in the crystalline form. If nitric or hydrochloric acid be added to fresh filtered urine, in the proportion of about 2 per cent. by volume, and the mixture allowed to remain at rest for twenty-four hours, the sides and bottom of the vessel become covered with a thin deposit of uric acid crystals. These crystals are usually transparent rhomboidal plates, with their obtuse angles rounded off, and tinged of a yellowish hue by the coloring matter of the urine. They are frequently arranged in radiated clusters, or small spheroidal masses, which vary in size and regularity, according to the time occupied in their formation.

Fig. 80.

Crystals of Uric Acid; deposited from urine, after the addition of nitric acid.

When the urine is scanty and concentrated, with a specific gravity of 1030 or 1035, but without abnormal ingredients, if mixed with half its volume of nitric acid and exposed to a low temperature, it will soon become filled with an abundant crystallization of nitrate of urea. In urine of this specific gravity, the water is still sufficient to hold the urea in solution, but allows a separation of nitrate of urea on the addition of nitric acid. This never takes place in urine of normal specific gravity.

Alkalies.—The addition of an alkali or alkaline carbonate to normal urine diminishes its acid reaction, and, when the point of saturation is reached, produces a turbidity, owing to precipitation of the earthy phosphates. These are the only ingredients of the urine liable to be thrown down by an alkali.

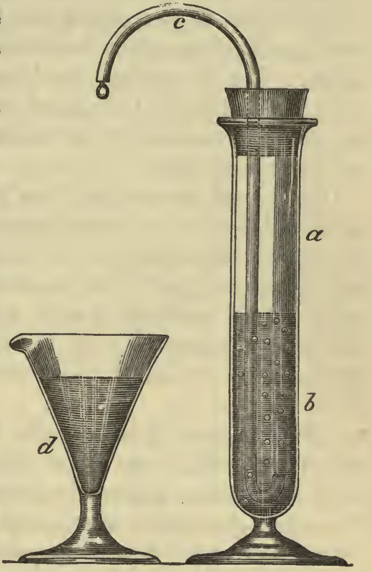
Mineral Salts.—Solutions of barium chloride, barium nitrate, or tribasic lead acetate, added to healthy urine, decompose its sulphates, producing a dense precipitate of the corresponding metallic salts. Solutions of silver nitrate produce a precipitate with the sodium and potassium chlorides, forming the insoluble silver chloride. Tribasic lead acetate and silver nitrate also throw down mucus and coloring matters.

Abnormal Ingredients of the Urine.

The abnormal ingredients which appear in the urine are either: 1st. Foreign substances accidentally present in the blood and eliminated by the kidneys, such as glucose, biliary matters, medicinal and poisonous substances; or 2d. The albuminous constituents of the blood, discharged with the urine owing to disturbance of the renal circulation.

Glucose.—The presence of glucose in the urine is characteristic of diabetes mellitus. In this disease the urine is generally increased in quantity and of unusually high specific gravity, namely, from 1035 to 1050. It is of a light straw color, and so transparent that it has the appearance of being dilute, though really denser than usual, owing to the glucose which it holds in solution. The glucose may be detected by Trommer's or Fehling's test, or by fermentation. For the latter purpose a little yeast is mixed with 15 or 20 times its volume of water, and the mixture allowed to remain at rest in an upright cylindrical vessel until the yeast globules have subsided to the bottom. The supernatant fluid, containing the soluble impurities of the yeast, is poured off, and a small quantity of the moist deposit added to the urine. The mixture is then placed in a ferment-apparatus and kept at a temperature of about 25° C., for forty-eight hours, when the gaseous products of fermentation will have been completely disengaged. The most convenient form of apparatus is a graduated test-tube, supported by a foot and provided with an India-rubber stopper, through which passes a narrow glass tube, open at both ends. Its inner extremity, reaching to the bottom of the test-tube, is bent upward, to prevent the escape of gas, while its outer portion is bent downward, to allow the liquid expelled through it to drop freely from its orifice. The test-tube being filled with the fermenting urine, the disengaged gas rises to its upper part and collects there, while the urine is forced out through the bent tube. Every cubic centimetre of carbonic acid produced corresponds to 0.26 milligrammes of sugar decomposed. A similar apparatus, containing the same quantity of healthy urine and yeast, should be kept at the same temperature for an equal time, as a comparative test; since a small quantity of gas might be produced from the yeast, owing to its imperfect purification. But in this case the disengagement of gas soon ceases; while in the fermenting solution it continues until all the sugar has been decomposed. This method does not give the precise quantity of glucose contained in any single specimen, since some of the urine escapes before fermentation is complete; but it is at the same time the surest indication of the presence of sugar, and a ready means of ascertaining its comparative amount in different specimens.

Fig. 81.



Ferment-Apparatus, containing saccharine urine in fermentation.—*a.* Upper part of the test-tube containing carbonic acid. *b.* Lower part of the test-tube containing the fermenting liquid. *c.* Bent glass tube, to allow the escape of liquid. *d.* Liquid which has been forced out from the test-tube by the accumulation of gas.

The quantity of glucose in a given specimen may be determined with sufficient accuracy for clinical purposes by the method of Roberts,* which depends upon the loss of specific gravity from the decomposition of glucose by fermentation. A portion of the urine is taken and its specific gravity ascertained at the temperature of 25° C. A little yeast is then added and the mixture kept at the same temperature until fermentation has ceased; when the specific gravity is again taken. The diminution in density caused by the decomposition of glucose is such that the loss of one degree in specific gravity indicates the disappearance of 2.197 milligrammes of glucose for every cubic centimetre of urine.

Glucose can be obtained from diabetic urine, according to the method of Hoppe-Seyler, by evaporating the urine over the water-bath to the consistency of a syrup, and allowing it to remain at rest until completely crystallized. The crystalline mass is triturated and washed with a small quantity of cold alcohol, to remove the urea. The residue is then extracted with boiling alcohol, and the alcoholic solution filtered while hot, after which the glucose is deposited in a crystalline form.

The glucose of diabetic urine is derived from the blood, from which it is eliminated in the renal circulation. It has been shown by Bernard,† that when glucose is injected into the blood-vessels or the subcutaneous connective tissue, the time within which it appears in the urine varies with the quantity injected and the rapidity of its absorption. If a solution of one gramme of glucose in 25 cubic centimetres of water be injected under the skin of a rabbit weighing a little over one kilogramme, it is destroyed in the circulation, and does not pass out with the urine. A dose of 1.5 gramme, injected in the same way, appears in the urine at the end of two hours, 2 grammes in an hour and a half, 2.5 grammes in an hour, and 12.5 grammes in fifteen minutes. When glucose accordingly accumulates in the circulation beyond a certain proportion to the volume of the blood, it is eliminated as a foreign substance, and appears in the urine.

Biliary Matters.—In some cases of jaundice, the coloring matter of the bile passes into the urine in sufficient abundance to give it a deep yellow or yellowish-brown tinge. Sodium glycocholate and taurocholate, according to Lehmann, have also been detected in the urine. In these instances, the biliary matters are reabsorbed from the hepatic ducts and conveyed by the blood to the kidneys.

Potassium ferrocyanide, when introduced into the circulation, appears with great readiness in the urine. According to Bernard, it may begin to be eliminated within twenty minutes after its injection into the duct of the submaxillary gland.

Iodine, in all its combinations, passes out by the same channel.

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* Urinary and Renal Diseases. Philadelphia edition, 1872, p. 198.

† Leçons de Physiologie Expérimentale. Glycogénie. Paris, 1855, p. 216.

After the administration, in man, of 192 milligrammes of iodine, in the form of syrup of the iodide of iron, we have found it in the urine at the end of thirty minutes; its elimination continuing for nearly twenty-four hours. In two patients who had been taking potassium iodide—one for six weeks, the other for two months—the urine still contained iodine three days after the last dose; but at the end of three days and a half it was no longer present. Iodine, as discharged by the urine, is always in the form of combination, from which it must be set free by the addition of a drop of nitric acid, after which it produces its characteristic blue color by admixture with starch. The same is true of other animal fluids, such as saliva and the perspiration, by which iodine is also eliminated after its introduction into the system.

Quinine, when administered as a remedy, has been detected in the urine. *Ether* passes out of the circulation in the same way, and its odor is sometimes perceptible in the urine, after being inhaled for the production of anæsthesia. The peculiar odors developed in the urine after the use of *Asparagus*, and certain other vegetable substances, are produced by a transformation of their ingredients while passing through the system.

Albumen.—Under ordinary conditions the albumen of the blood does not pass out from the renal vessels; but when the local pressure is increased beyond a certain point, owing to congestion, compression of the renal veins by abdominal tumors, pregnancy, or altered nutrition of the kidneys in Bright's disease, the albuminous ingredients of the blood transude through the capillaries and make their appearance in the urine.

Albuminous urine is usually pale, and often opalescent from the admixture of exfoliated epithelium cells or of fibrinous casts from the uriniferous tubules. In these cases, it should be rendered transparent by filtration before applying the tests, since the turbidity already existing might mask the reaction of albumen, if present in small proportion.

In albuminous urine with an acid reaction, the application of heat produces a turbidity which is in proportion to the quantity of albumen present. In extreme cases it may solidify, like the serum of blood, before reaching the boiling point; but more frequently the albumen is thrown down in loose whitish flakes. When the turbidity produced by boiling is moderate in amount, it may resemble that due to precipitation of the earthy phosphates. It can, however, be distinguished by the addition of a drop of free acid, which at once redissolves the phosphates, but does not affect a turbidity caused by albumen. An albuminous precipitate, on the other hand, however abundant, is redissolved by the addition of a caustic alkali.

If the urine be alkaline in reaction, boiling may not throw down its albumen, this substance being soluble in an alkali. Alkaline urine, accordingly, if suspected of being albuminous, should be rendered distinctly acid before boiling, by the addition of a small quantity of a free acid.

Nitric acid, added in moderate quantity to albuminous urine, produces a turbidity by coagulating the albumen. Alcohol, in equal volume, will have the same effect; and a solution of potassium ferrocyanide, acidulated with acetic acid, will also produce coagulation. When all these tests have been applied, no doubt will remain as to the presence or absence of albumen.

Deposits in the Urine.

The deposits which appear spontaneously in the urine consist either: 1st, of some of its normal ingredients, thrown down in consequence of a change in its composition; or 2d, of exudations from the urinary passages, owing to diseased local conditions. Those belonging to the first class are the earthy phosphates and the urates. The most common of those belonging to the second are blood, mucus, and pus.

Deposits of the Earthy Phosphates.—These deposits are always of a white color, and are seldom abundant. When the urine is first passed, they are disseminated through its mass in the form of a light cloudiness, which settles slowly to the bottom of the vessel. The urine is alkaline or neutral in reaction, and is usually of less than the average specific gravity. The precipitate is amorphous, presenting no crystalline forms under the microscope. It is at once redissolved on the addition of an acid, and presents all the chemical reactions belonging to the earthy phosphates. The alkaline condition of the urine, causing this deposit, may be due to temporary diminution in the quantity of uric acid produced in the system, or to a formation of alkaline carbonates from the use of fruits or vegetables containing salts of the vegetable acids.

Deposits of the Urates.—The urates appear as a deposit when their formation in the system is unusually abundant in proportion to the urine, so that they are no longer held in solution. The urine is nearly always concentrated, highly colored, above the average specific gravity, and of a strongly acid reaction. The deposit is sometimes nearly white, but usually of a light pink or even red color, according to the concentration of the urine. If allowed to settle in a white porcelain vessel, and the supernatant fluid poured off, the deposit is sometimes left as a brick-red stain on the inner surface of the vessel, forming what is known as the "brick-dust" sediment.

Deposits of the urates are recognized by the two following characters. First, they never appear while the urine is still warm, but only after it has cooled; the urine, when first passed, being always perfectly clear, and becoming turbid on repose. Secondly, the urine, however turbid, if heated in a test-tube, becomes again clear, usually before reaching the boiling point. Both these characters depend on the solubility of the urates at high temperatures.

In rare cases, when urine is turbid with the urates and also contains albumen, a double effect may be produced by the application of heat. When the specimen is first heated, it clears up, owing to the solution of the urates; but, on approaching the boiling point, it again becomes turbid from precipitation of the albumen.

The urates are also soluble in caustic alkalies, and the addition of a few drops of a solution of sodium or potassium hydrate redissolves the precipitate. Free acids, on the other hand, decompose it, with the formation of a corresponding sodium or potassium salt, which remains in solution, and the separation of uric acid, which slowly crystallizes. But the volume of uric acid produced is so much smaller than that of the urates previously disseminated through the urine, that the only effect immediately apparent is that of solution of the precipitate. A deposit of the urates is accordingly the only one liable to occur in the urine, which is cleared up by both alkalies and acids.

Deposits of the urates, when first thrown down, are pulverulent in form, presenting under the microscope the appearance of minute granules. After a day or two they sometimes crystallize in globular masses of radiating needles, often with straight or curved projections from the outer surface. If a free acid be added to this deposit, the crystalline masses grow transparent, and slowly dissolve from without inward, while rhomboidal tabular crystals of uric acid appear in the adjacent fluid.

FIG. 82.

CRYSTALLINE MASSES OF SODIUM URATE, from a urinary deposit.

Crystals of uric acid sometimes appear in a deposit of the urates after a few hours, owing to the development of a free acid in the urine; and they are sometimes formed within the urinary passages, so as to be present in the urine when passed. Owing to their density and angularity they cause an irritation to the mucous membrane of the bladder and urethra, and are known as the "gravel" of the urine. In a mingled precipitate of the urates and uric acid, the uric acid is a scanty, dense, deeply colored, crystalline deposit which sinks rapidly and accumulates at the bottom of the vessel, while the comparatively light and pulverulent urates are more slowly deposited above it.

Blood.—Urine containing blood is more or less tinged throughout with a dull reddish color. After one or two hours of repose in a cylindrical vessel, the blood-globules are slowly deposited; and the minute filamentous coagula with which they are frequently entangled form a strongly colored red layer at the bottom of the vessel. The nature of the deposit is recognized by two well-marked characters, namely: 1st. The blood-globules are distinguished by microscopic examination, their form not being entirely lost even after remaining in the urine for several hours; and 2d. The supernatant fluid, when decanted, is found to contain albumen.

Mucus.—The slight quantity of vesical mucus, normally contained in the urine, is at first uniformly disseminated throughout its mass, and even after being left in repose is insufficient to produce any well-marked or consistent deposit. The light cloudy opalescence, which it forms at the bottom of the vessel, is visible only on close inspection, and is readily disseminated again by agitation. But in inflammation of the urinary bladder, the mucus is increased in quantity and altered in quality. It then appears as a consistent mass, which does not mix uniformly with the urine, but subsides to the bottom as a semifluid deposit. Mucus by itself is transparent and colorless, but it frequently contains epithelium cells from the bladder; and when crystalline or pulverulent deposits take place in the urine, they first appear in contact with the mucus, so that its surface is often sprinkled with the urates or phosphates. A deposit of mucus is distinguished by its viscid and semifluid consistency. It is not affected by heat, but is coagulated and shrivelled by alcohol and by nitric or acetic acid. Urine containing mucus is liable to rapid decomposition, and often has a peculiarly offensive odor from this cause.

Pus.—When pus is contained in the urine it gradually subsides if allowed to remain at rest, forming a dense, creamy-white deposit, perfectly fluid in consistency and easily disseminated by agitation. Microscopic examination shows it to be composed of colorless, granular, nucleated "pus-globules," identical in appearance with the white globules of the blood, but distinguishable from those belonging to a deposit of blood by their abundance and by the absence of red globules. If the supernatant fluid be poured off, and a few drops of a solution of caustic alkali added to the deposit, it loses its white color and opacity, owing to the solution of its granular cells, and swells up into a transparent, colorless gelatinous substance, which can no longer be poured off in drops, but slides out of the vessel in a single semi-solid mass. This character will serve to distinguish a purulent deposit from any other liable to occur in the urine. The supernatant urine, when filtered, is found to contain a small quantity of albumen, the interstitial fluid of pus being itself albuminous.

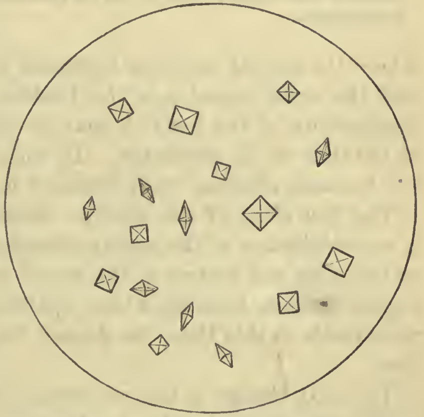
Decomposition of the Urine.

After its discharge from the body, the urine undergoes spontaneous changes, by which its organic ingredients are altered and finally disappear. This decomposition is closely dependent on the mucus in the urine, being much retarded if this be separated by immediate filtration, and hastened in a corresponding degree when the mucus is abnormally abundant. It is characterized by two different stages, distinguished by the successive development of acid and alkaline products. They are known respectively as the acid and the alkaline fermentations.

Acid Fermentation of the Urine.—This process takes place for the most part within twelve, twenty-four, or forty-eight hours after the discharge of the urine. It consists in the production of a free acid, usually lactic acid, from some undetermined organic ingredients of the excretion. The urine when fresh contains no free acid, its reaction being due to the presence of sodium biphosphate. But lactic acid has so often been found in urine as to be sometimes regarded as one of its normal constituents. Observation, however, has shown that urine, though free from lactic acid when first passed, may present distinct traces of this substance after some hours of exposure to the air. Its production in this way, though not constant, appears sufficiently frequent to be regarded as a normal process.

There is reason to believe that oxalic acid is sometimes produced in a similar manner. A deposit of lime oxalate is frequently present in the urine a day or two after its discharge, without the existence of any perceptible morbid symptom. Whenever oxalic acid is formed in the urine it unites with lime in preference to any other of the bases present, and is consequently deposited under the form of lime oxalate, which is quite insoluble in urine, even at the boiling point. In these cases, the lime oxalate crystals gradually appear in the light cloud of mucus at the bottom of the vessel. They are of minute size, for the most part just visible to the naked eye, scanty in amount, transparent, and colorless. They have the form of regular octohedra, or double quadrangular pyramids, united base to base. They usually show themselves about the second day, the urine continuing clear and retaining its acid reaction; and they frequently appear as a deposit when no substance containing oxalic acid or oxalates has been taken with the food. The precise source of the oxalic acid, under these circumstances, has not been determined, but it is probably derived from a partial metamorphosis of the uric acid. If uric acid be boiled in two parts of water with lead peroxide, it is decomposed, with the production, among other substances, of oxalic acid; and it is supposed that some similar change may take place in the urine, causing the appearance of oxalic acid in minute quantity. This decomposes a portion of the lime salts, and consequently appears as a crystalline deposit of lime oxalate.

Fig. 83.



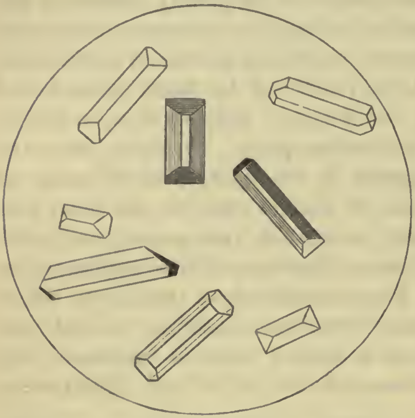
Crystals of Lime Oxalate, deposited from healthy urine, during the acid fermentation.

Alkaline Fermentation of the Urine.—After a few days the changes above described come to an end, and are succeeded by the transformation of urea into ammonium carbonate. This change, which may be artificially produced in a watery solution of urea by continued boiling, takes place in the urine slowly at low temperatures, more rapidly during warm weather. The elements of two molecules of water unite with those of urea to produce ammonium carbonate, as follows:

$$\underset{\text{Urea.}}{CH_4N_2O} + 2H_2O = \underset{\text{Ammonium carbonate.}}{(NH_4)_2CO_3}$$

The ammoniacal salt when first produced neutralizes a corresponding quantity of sodium biphosphate, diminishing the acid reaction of the urine. This diminution continues, as the fermentation proceeds, until the acidity disappears altogether. The urine then becomes neutral, and subsequently alkaline; its alkalescence growing more pronounced with the accumulation of the ammoniacal salt.

Fig. 84.



Crystals of Ammonio-Magnesian Phosphate, deposited from healthy urine, during the alkaline fermentation.

The time at which the urine becomes alkaline varies with its original degree of acidity and the rapidity of its decomposition. Urine which is neutral at the time of its discharge, becomes alkaline more rapidly than that which has at first a strongly acid reaction. In summer, it is often alkaline on the third, fourth, or fifth day; while in winter, if kept in a cool place, it may still be neutral at the end of fifteen days. In paralysis of the bladder with cystitis, where the vesical mucus is increased in quantity and altered in quality, and the urine remains in the bladder for ten or twelve hours at the temperature of the body, it may be distinctly alkaline and ammoniacal at the time of its discharge. In these cases it is acid when secreted, but becomes alkaline while retained in the bladder.

The first effect of the alkaline condition of the urine, thus produced, is a precipitation of the earthy phosphates. This deposit slowly settles on the sides and bottom of the vessel, or is partly entangled with certain animal matters, forming a thin, opaline scum on the surface. There are no crystals at this time, the deposit being entirely amorphous and granular.

The next change is the production of a new salt, the *ammonio-magnesian phosphate*, by the combination of ammonia, formed from urea, with the magnesium phosphate already present in the urine. This change is represented as follows:

$$\underset{\text{Magnesium phosphate.}}{MgHPO_4} + \underset{\text{Ammonia.}}{NH_3} = \underset{\text{Ammonio-magnesian phosphate.}}{MgNH_4PO_4}$$

The crystals of this salt show themselves throughout all parts of the mixture, entangled in the mucus at the bottom, adhering to the sides of the vessel, and scattered over the film on the surface of the urine. By their refractive power they give to this film a glistening and iridescent appearance, nearly always visible at the end of six or seven days. They are colorless, transparent, triangular prisms, generally with bevelled extremities, their edges and angles frequently replaced by secondary facets. They are insoluble in alkalies, but are easily dissolved by acids, even very dilute. At first they are of minute size, but gradually increase, so that after seven or eight days they may be recognized by the naked eye.

As decomposition proceeds, the ammonium carbonate, after saturating all the other ingredients with which it is capable of uniting, begins to be given off in a free form. The urine then acquires an ammoniacal odor; and a piece of moistened test-paper, held above its surface, will be turned by the escaping alkaline gas. This is the source of the ammoniacal vapor given off wherever urine is allowed to remain and decompose. The change continues until all the urea has disappeared.

SECTION III.

THE NERVOUS SYSTEM.

CHAPTER I.

GENERAL STRUCTURE AND FUNCTIONS OF THE NERVOUS SYSTEM.

THE nervous system is an apparatus of communication, by which the various parts of the body are brought into relation with each other, and different organs excited to harmonious or alternating action. Its effects are produced by an influence transmitted from one region to another, stimulating or modifying the animal functions according to the requirements of the system at large. It differs in its properties and mode of action from the other anatomical structures of the body, to which it is superadded for their regulation and control.

The specific physiological properties or modes of activity, belonging to a bodily organ, may often be called into operation by a direct stimulus or exciting cause. The poles of a galvanic battery, applied to the muscles of a frog's amputated leg, produce contraction and movement; a solution of atropine dropped on the cornea of a living animal, when absorbed and brought in contact with the iris, causes a change in the condition of its fibres and a dilatation of the pupil; and if the heart of a frog, after removal from the body, be touched with the point of a needle, it repeats the movement of an ordinary pulsation. In these instances, the physiological act is in response to a stimulus operating directly on the tissues of the organ.

But this is not the mode in which the animal functions are excited during life. The stimulus which calls into action the living organs is not direct, but indirect, in its operation. In the normal condition, the muscles are never made to contract by an external stimulus applied to their own fibres, but by one which operates on some other organ, adjacent or remote. The functional activity of the glands is increased or diminished by causes acting on other parts; as where a flow of saliva from the parotid is produced by food introduced into the mouth, or where the cutaneous perspiration is modified by mental conditions. The various organs are thus connected with each other by a mutual sympathy which regulates their physiological action; and this connection is established by means of the nervous system.

The function of the nervous system is therefore *to associate the different parts of the body in such a manner, that stimulus applied to one organ may excite the activity of another.*

The instances of this action are almost as numerous as the vital phenomena. The light falling upon the retina produces contraction of the pupil. Introduction of food into the stomach causes a discharge of bile from the gall-bladder. Alimentary substances, in contact with the mucous membrane of the intestine, excite the peristaltic action of its muscular coat; and the presence of a fœtus in the uterus is accompanied by increased growth of the mammary glands. Every organ is subservient, in the manifestation of its activity, to influences derived from other parts through the nervous system.

In the nervous system there are two kinds of anatomical elements; namely, *nerve fibres* and *nerve cells.* The nerve fibres are the characteristic constituents of the "white substance," forming the mass of the nerves and their ramifications, the external portion of the spinal cord, and much of the internal parts of the brain. The nerve cells are found in the "gray substance," which constitutes the external or convoluted layer of the brain, as well as various internal deposits near its base, the central portions of the spinal cord, and many small detached masses, or ganglia, in different parts of the body.

Nerve Fibres.

The nerve fibres are cylindrical filaments, arranged in bundles or tracts, for the most part parallel with each other. Their diameter varies considerably, even in the same locality; some of the fibres in a single bundle being 10, 15, or 18 micro-millimetres in diameter, while others are not more than 2.5 mmm. Their average size also varies in different parts of the nervous system. The larger fibres are found in the peripheral trunks and branches of the nerves, where they have an average diameter of 12.5 mmm.; in the white substance of the brain and spinal cord their average diameter is 5 mmm., and in the gray substance it is reduced to 2 mmm. Certain portions of the nervous system are distinguished by the comparative abundance of their larger or smaller fibres. Thus in the cutaneous nerves of man, according to Bidder, Volkmann, and Kölliker, the larger and smaller fibres are in about equal quantity, while in the muscular nerves the larger fibres are three times as abundant as the smaller. In the nerves of bony tissue the number of small fibres is double that of the large ones; and in the gray substance of the cerebral hemispheres they all belong to the smaller variety, none being larger than 6 or 7 mmm. in diameter. The nerve fibres in the same bundle or tract may increase or diminish in size at different parts of their course; as Kölliker has shown that the fibres of the posterior roots of the spinal nerves, in passing to the gray substance of the cord, are reduced in average diameter from 10 to 5 mmm., and those of the white substance of the cerebral hemispheres, on entering the gray matter of the convolutions, are reduced from 5 to 2 mmm. in diameter.

The nerve fibre, in its most complete form, presents three distinct structural elements, namely: an external tubular sheath, an intermediate medullary layer, and a central axis cylinder.

The Tubular Sheath.—The nerve fibre consists externally of a colorless, transparent, tubular membrane, known as the "sheath of Schwann," which closely invests its remaining portions. This membrane may often be distinguished at points where the fibre has been accidentally compressed or indented; or it may be brought into view according to the method of Kölliker, by treating the fibres with a cold solution of sodium hydrate, and afterward boiling them for an instant in the same fluid. This extracts the greater part of their contents, and leaves the sheath in the form of an empty cylindrical canal. In its general character, the tubular sheath resembles the sarcolemma of muscular fibre, its principal physical properties being its cohesion and elasticity. . Its office is no doubt that of a protecting envelope, by which the internal portions are maintained in the cylindrical form.

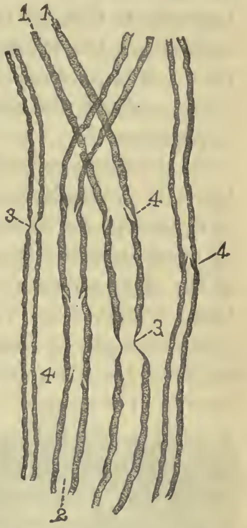
The Medullary Layer.—Immediately within the tubular sheath is a layer of transparent, highly refractive material, nearly oleaginous in consistency, termed the "medullary layer," or myeline, which gives to the nerve fibres, and the tracts composed of them, their white glistening aspect. Owing to the presence of this substance, the nerve fibre has, under the microscope, a characteristic double contour, presenting two parallel outlines on each border; indicating the external and internal limits of the medullary layer. The fibres containing a medullary layer, and exhibiting its characteristic double contour, are called "medullated nerve fibres."

The medullary layer is readily altered by the imbibition of water. It swells up and exudes from the divided extremities of the nerve fibres, in filamentous tufts and masses of irregular outline, which from their peculiar appearance are known as "myeline forms." These masses become mingled with each other when a number of divided or lacerated nerve fibres have been placed in water; and the myeline is after a time so much altered and distorted, by the imbibition extending to the interior of the fibre, as to obscure all its remaining anatomical characters.

Owing to this alterability of the nerve fibres it has been found of advantage to study them with the aid of various staining and hardening liquids; one of the most useful of which is perosmic acid. Dilute solutions of this substance fix the nerve fibres in their natural form and position, so that they can afterward be manipulated with less danger of injury; and it moreover stains the medullary layer of a blackish hue, without coloring the remaining elements. When a group of nerve fibres, stained by perosmic acid, are viewed in transverse section, each fibre appears as a dark zone enclosing a transparent, colorless space near its centre; the dark exterior zone being the blackened medullary layer, while the central space represents the uncolored axis cylinder. When viewed in profile, such fibres exhibit a dark colored double border, formed by the medullary layer, surrounding the longitudinal axis cylinder.

In regard to its physiological function, the medullary layer is considered by some writers as an isolating substance, like the gutta-percha envelope of a submarine telegraph wire, to confine the transmission of nerve force within proper limits, and prevent its diffusion to neighboring parts. It certainly does not act directly in this transmission; since, as hereafter shown, it is interrupted at numerous points in the course of the fibres; and it is always wanting for some distance in the neighborhood of both their origin and their termination. These facts are also at variance with its supposed character as an isolating material; since any discontinuity of its substance would seem to destroy its efficiency for that purpose. It is sometimes regarded, with perhaps greater plausibility, as affording, by its consistency, a physical protection to the axis cylinder; securing it from local injury, in flexions or indentations, by the uniform support which a fluid envelope would give. Its interruptions during the course of the nerve fibres are not sufficient to interfere with its usefulness in this respect.

Fig. 85.



Nerve Fibres, fixed and stained by perosmic acid; from the posterior wall of dorsal lymph-sac of Frog. —1, 1, Medullary layer. 2, Axis Cylinder. 3, 3, Constrictions of Ranvier. 4, 4, Incisions of Schmidt.

The Axis Cylinder.—The central part of the nerve fibre consists of a pale, homogeneous, or finely granular cord, of nearly cylindrical form, situated in its longitudinal axis. From these characters it has received the name of the "axis cylinder." In consistency the axis cylinder is a soft solid, and, though very delicate, it has a certain degree of elasticity. By some observers (Schultze, Gerlach) it is regarded as composed of minute fibrillæ, united into a uniform bundle; by others of equal authority (Kölliker) the indications of its fibrillated constitution are considered as uncertain.

The axis cylinder consists of an albumenoid substance, insoluble in water, alcohol, and ether. It becomes pale and swollen by the action of concentrated acetic acid, and is readily dissolved by a boiling solution of sodium hydrate. It is stained red by solutions of carmine, which, on the other hand, produce no effect on the medullary layer; and after the use of this agent, the transverse section of a nerve shows in the interior of each fibre a red or pinkish spot in the place of the axis cylinder, surrounded by a colorless zone representing the medullary layer. In nerve fibres treated with a solution of gold chloride and subsequently exposed to light, the axis cylinder is stained of a dark purple, nearly black color; and by this mode of preparation nerve fibres of extreme delicacy may be traced where they would otherwise escape observation.

In its physiological properties, the axis cylinder is beyond question the essential element of the nerve fibre. By its abundant albumenoid ingredients it is distinguished from the medullary layer, and it forms exclusively the whole of the fibre both at its origin and its termination. It is no doubt through the axis cylinder that the nerve current is transmitted, the remaining portions of the fibre being of secondary importance.

Of the three constituent parts of the nerve fibre, the axis cylinder is the only one uniformly continuous throughout. At frequent intervals in its course the fibre presents a remarkable diminution in size, caused by an annular constriction of the sheath of Schwann and an interruption at the same point of the medullary layer (Fig. $85_{3,3}$). These constrictions, which, from the name of their discoverer, are known as the "constrictions of Ranvier," recur in general at distances of about 75 or 80 times the diameter of the nerve fibre. At each of these points the sheath of Schwann contracts to about one-half its ordinary calibre, leaving a diminished orifice through which the axis cylinder passes, while the medullary layer terminates on each side by a rounded extremity. The portion of a nerve fibre included between two consecutive annular constrictions, is called an "inter-annular segment."

The annular constrictions visible in nerve fibres have been often attributed to mechanical injury, or to the action of fluids used in their preparation; but, as Ranvier has shown, they may be seen, without the addition of any reagent, in the uninjured nerve fibres of the frog's lung, while the circulation of the blood is still going on. They are consequently a normal anatomical feature of the nerve fibre.

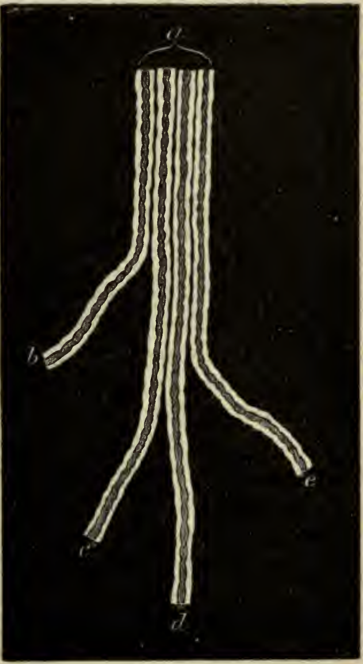
Beside the annular constrictions, there are other partial or complete interruptions of the medullary layer, of more frequent occurrence, situated at irregular intervals in the length of each inter-annular segment. These are the "incisions of Schmidt" (Fig. $85_{4,4}$). In a profile view of the nerve fibre they present the appearance of narrow oblique cuts in the medullary layer, extending from its outer surface nearly or quite to its internal border. Both the annular constrictions and the incisions of Schmidt are most distinctly recognized after partial staining of the medullary layer with perosmic acid.

Non-medullated Nerve Fibres.—Beside the nerve fibres above described, there is a second variety, distinguished by the absence of a medullary layer, and termed "non-medullated nerve fibres." They are the only nerve fibres to be found in invertebrate animals; and in man and the vertebrate animals they are mingled in various proportions with medullated fibres in different nerves. The olfactory nerve consists exclusively of non-medullated fibres; there are none, on the other hand, in the optic nerve, which is composed altogether of the medullated variety. Among the peripheral nerves, non-medullated fibres are most abundant in those of the sympathetic system, where they were first discovered, and where they often constitute a majority of all the nerve fibres present. In the trunks and branches of the cerebro-spinal system they are much less numerous, but vary in proportion in different nerves and in different species of animals. In all cases, nerves consisting mainly or exclusively of medullated fibres have an opaque, white, glistening aspect, due to their myeline; while those containing non-medullated fibres are grayish or semitransparent, according to the proportion of these fibres in their tissue.

All the medullated nerve fibres lose their myeline and become non-medullated shortly before their termination in the muscular tissue or the organs of sensibility; and they are also non-medullated at and near their termination in the gray matter of the brain and spinal cord. In these situations the nerve fibre is reduced to a simple axis cylinder, by which it is connected with the peripheral and central organs of the nervous system.

Course and Mutual Relation of the Nerve Fibres.—In the white substance of the brain and spinal cord the nerve fibres form continuous tracts, lying in close apposition with each other, enveloped only by a delicate granular and finely fibrillated intervening material. But on emerging from the bony cavities of the cranium and vertebral canal, they are collected into distinct bundles, each invested by a lamellated sheath of fibrous connective tissue, and enclosed in a larger compound mass by a common fibrous sheath or "neurilemma." Such a compound bundle is called a *nerve*, and the fibres which it contains are distributed, after a longer or shorter transit, usually to associated organs or adjacent regions of the body.

FIG. 86.



DIVISION OF A NERVOUS BRANCH (*a*), into its ultimate fibres, *b*, *c*, *d*, *e*.

So far as our observation extends, the individual nerve fibres, as a rule, are continuous and independent, from their origin in the nervous centres to within a short distance of their peripheral termination. When a nerve divides into several branches, or when adjacent nerves communicate by inosculation, as in the cervical, brachial, or lumbar plexuses, it is because certain fibres leave those with which they were associated and pursue a different course. A nerve which originates, for example, from the spinal cord, and passes down the arm to the muscles and integument of the hand, contains at its origin all or nearly all the fibres, which it afterward gives off in branches and ramifications; and the inosculation of two nerves is effected by some of the fibres from one passing over to join the other, while some of those belonging to the second may also cross and join the first. In whatever way, therefore, the nerve fibres are associated in the trunks and branches, each may still preserve its specific and independent action.

A nerve usually consists of several distinct bundles of fibres, each bundle enveloped in its lamellated sheath; and when the bundle, after its separation from the trunk, divides into secondary branches, each branch is covered by a thinner lamellated sheath, an offshoot from that of the parent bundle. These sheaths are lined by a layer of flattened polygonal endothelial cells, like those on the inner surface of the blood-vessels. As the branches are reduced in size by repeated subdivision, their sheaths become thinner in the same proportion, by a diminution in the number of lamellæ of which they are composed; and in those containing but few nerve fibres, the sheath consists of a single endothelial layer. This transparent envelope, surrounding the smallest ramifications of the nerves, is known, from the name of its discoverer, as the "sheath of Henle." Each individual nerve fibre, after separating from the rest, to run an independent course, is also accompanied by such a sheath, of about double its own diameter, in which it lies, surrounded by lymph or a lymph-like fluid.

An isolated nerve fibre, passing through the tissues toward its termination, is therefore covered by two envelopes, quite distinct from each other. One is its tubular membrane, or "sheath of Schwann," which is part of the fibre and closely invests its surface; the other is the "sheath of Henle," which is an adventitious tube, of larger size, and separated from it by an appreciable space.

Peripheral Termination of the Nerve Fibres.—Near their peripheral termination, the nerve fibres present certain important modifications both in structure and arrangement.

First, the smaller branches, or bundles of nerve fibres, after penetrating the tissues, suddenly divide and subdivide with unusual rapidity; and these subdivisions, uniting with each other by inosculation, form *plexuses*, from which are given off individual fibres to supply the anatomical elements of the tissues. In the skin there are two such plexuses, a deeper and a more superficial, of which the latter is the more closely set and composed of smaller bundles, containing only one or two fibres each. As a rule, in all tissues, the second or terminal plexus is the finest, inclosing between its meshes the narrowest interspaces. The nerve fibres, on reaching the terminal plexus, are also reduced in size, being diminished both in the skin and in the muscles from 10 or 15 mmm. to 4 or 5 mmm. in diameter. According to Kölliker it is sometimes possible to observe a diminution in size of single nerve fibres in different parts of the muscular tissue.

Secondly, both in the terminal plexus and in the branches given off from them, the *nerve fibres themselves undergo division;* so that a single fibre in this situation may give rise to two or more branches, each branch retaining all the original anatomical characters of the nerve fibre. Such a division of nerve fibres, according to Ranvier,* is occasionally visible in the smaller trunks and branches, as in those of the spleen and even sometimes in the muscular nerves; but in general it only occurs in the immediate neighborhood of their final distribution. Here, on the other hand, it is very frequent. The division always takes place at an annular constriction. The axis cylinder divides, usually at an acute angle, into two or more secondary axis cylinders, each of which becomes at once enveloped by a medullary layer, like that above the constriction; and each secondary nerve fibre is at first nearly or quite equal in diameter to that from which it was derived. But after several successive divisions the fibres are diminished in average diameter; and at the same time the annular constrictions are more frequently repeated. In the small nerve fibres, accordingly, near their peripheral termination, the inter-annular segments are shorter and more numerous than in the large fibres of the nervous trunks and branches.

A nerve fibre may thus pass undivided throughout the roots, trunk, and principal branches and ramifications of the nerve, and may then, shortly before its termination, break up into a number of separate but closely adjacent secondary fibres. It has been estimated by Reichert, that, in the subcutaneous muscles of the frog, one primitive fibre may give rise by its division to about 30 terminal extremities.

Fig. 87.

Division of a Nerve Fibre; from pulmonary membrane of frog's lung.

Thirdly, the nerve fibre, near its peripheral extremity, loses its medullary layer, and, consequently, its double contour. As the sheath of Schwann also disappears, the nerve fibre finally consists only of the axis cylinder, which near its extreme point of termination sometimes exhibits a fine longitudinal striation, indicating the existence of minute fibrillæ united with each other.

The termination of nerves in the *sensitive integument* has been most successfully studied in the "Pacinian bodies" of the skin and mesentery, and in the "end-bulbs" of the conjunctiva. In these bodies, both in man and animals, there is a general resemblance in the arrangement of the parts, together with variations of detail in different species and different situations. They all consist of an ovoidal-shaped mass, surrounded by single or multiple capsules, which are expansions of the lamellated sheath of the nerve branch supplying them, or of the sheath of Henle accompanying its finest ramifications. They

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* Histologie du Système Nerveux. Paris, 1878, tome ii., pp. 109, 268.

contain a fluid or semifluid interstitial substance, in which the terminal nerve fibre is enclosed and in which it ends, either by expansion into the so-called "terminal buds," or by the indefinite disappearance of its fibrillæ.

The Pacinian bodies of the hands and feet in man, and in corresponding situations in many of the quadrupeds, are from 1 to 4.5 millimetres in length. Their substance is enclosed in numerous concentric capsules, each of which, according to Key and Retzius,* is a continuation of the lamellated sheath of the nerve-branch, and is furnished with a double layer of polygonal nucleated endothelial cells, like those in the lamellated sheath itself. At the central part of the Pacinian body the capsules are absent, leaving a narrow elongated space, known as the "interior bulb," surrounded by an endothelial layer continuous with that of the sheath of Henle. Into this interior bulb the ultimate nerve fibre penetrates, often after repeated division of its parent fibre, and at the same time becomes divested of its medullary layer. The cylinder axis then runs longitudinally through the central part of the interior bulb toward its peripheral extremity, where it exhibits a fibrillated appearance, and ends in one or more fungus-like tufts, or "terminal buds," which appear like radiated expansions of its component fibrillæ.

Fig. 88.

Peripheral Extremity of the Interior Bulb of a Pacinian Body; showing the fibrillated texture of the axis cylinder and its terminal buds. (Key and Retzius.)

The end-bulbs in the conjunctiva are similar in form to the Pacinian bodies, but of much smaller size, measuring in man from one-third to one-half a millimetre in length. They have only a single capsule, continuous with the sheath of Henle accompanying the nerve fibre. The nerve fibre, as in the foregoing description, loses its medullary layer after reaching the base of the bulb, and enters its interior as a pale, slender axis cylinder. In the calf, the axis cylinder sometimes runs nearly straight through the bulb toward its farther extremity, where it terminates in a fungus-like tuft, like those of a Pacinian body. In man, it makes a number of turns within the bulb, where it finally disappears, apparently by dispersion of its fibrillæ.

The termination of nerve fibres in *muscular tissue* has been studied in many animals, both in the fresh condition and with the aid of staining and hardening preparations. No one of these methods has been found to demonstrate fully the anatomical features of the nervous termination; but by combining the results obtained from all, histologists have acquired a certain degree of knowledge in this respect, which may be summed up as follows. In general, a striped muscular fibre is supplied with only a single ultimate nerve fibre; but this nerve fibre, on

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* Anatomie des Nervensystems und des Bindegewebes, Stockholm, 1876. Zweite Hälfte, p. 176.

passing beneath the sarcolemma, divides into a terminal arborization, which lies in contact with the striated muscular surface. The stimulus conveyed through a single nerve fibre is thus communicated to the contractile substance of the muscle at many different points. With the exception of some variations of form in different species, the details of the muscular termination of nerve fibres are essentially the same in reptiles, birds, and mammalians. As the ultimate nerve fibre reaches the point of its attachment to the muscle, the sheath of Henle, with which it was surrounded, leaves it and becomes continuous with the sarcolemma. At the same time its medullary layer terminates, in the usual way, at an annular constriction. That portion of the nerve fibre immediately outside the sarcolemma is its last inter-annular segment; and within the sarcolemma the axis cylinder is destitute of myeline. At this situation the axis cylinder breaks up into its terminal arborization; and it is the form, direction, and frequency of these ramifications which constitute the main differences in this respect between different animals. Each member of the terminal arborization is surrounded by a light zone of granular matter, in which large flat oval nuclei, with well-marked nucleoli, are imbedded. The only parts of the nerve fibre therefore in immediate contact with the contractile muscular substance are those derived from the ramification of its axis cylinder.

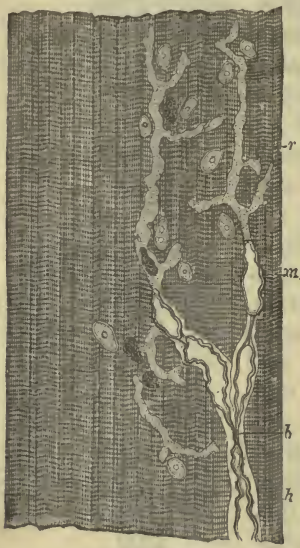
Physiological Properties of the Nerve Fibres.—The nerve fibres are channels of communication between the nervous centres on the one hand and the peripheral organs on the other. For this purpose they are endowed with a special irritability by which, when excited at one end, they transmit the impulse throughout their entire length, and produce an effect at the opposite extremity. Those distributed to the skin, when excited at the periphery, produce in the brain a corresponding sensation. On the other hand, those distributed to the muscles, when excited at their origin by the impulse of the will, cause contraction in the muscular fibres. This action produces no visible change in the nerve

FIG. 89.

SENSITIVE NERVE FIBRE AND END-BULB; from the conjunctiva of man. The turns of the axis cylinder, within the bulb, are exhibited in various transverse and oblique sections. (Key and Retzius.)

fibre, its effects being manifest only in the organs where it terminates. Nevertheless, it is evident that the fibre serves to communicate in some way an action from one extremity to the other; since, if it be divided in any part of its course, the communication ceases, and sensation can no longer be perceived from impressions made on the skin, nor voluntary contraction excited in the muscles.

Fig. 90.



Nervous Termination in a Muscular Fibre of the Green Lizard. —*h*, Sheath of Henle, surrounding the nerve fibre. *b*, Annular constriction, and division of the nerve fibre. *m*, Last interannular segment *r*, Terminal arborization of axis cylinder beneath the sarcolemma. (Ranvier.)

Owing to the different effects thus produced at their extremities, the nerves and nerve fibres are distinguished by different names. Those which transmit the stimulus of sensation, from the periphery to the centre, are called *sensitive* nerves or nerve fibres; those which transmit the stimulus of motion, from the nervous centre to the muscles, are called *motor* nerves or nerve fibres. As a rule, both sensitive and motor fibres are associated in the same bundle, and separate from each other only near their final distribution. But in some situations, near the origin of the nerves as well as near their termination, the sensitive and motor fibres run in distinct bundles; as, for example, in the two roots of the fifth pair of cranial nerves, and in those of the spinal nerves generally. The fibres belonging to the facial nerve are all motor fibres, making this exclusively a motor nerve. Those branches of the fifth pair, on the other hand, which are distributed to the integument and mucous membranes of the face, are exclusively sensitive; while the branch of the same nerve distributed to the muscles of mastication consists principally or entirely of motor fibres.

No essential distinction is perceptible, in anatomical characters, between sensitive and motor nerve fibres. In nerves which perform a motor function, the fibres are for the most part of comparatively large size, averaging 15 mmm. in diameter; while in those performing a sensitive function they are smaller, averaging not more than 10 mmm. in diameter, and many of them being considerably less. But this is only a difference of numerical proportion between the larger and smaller fibres; since both large and small fibres are found in both motor and sensitive nerves. Even the motor fibres become reduced to the smaller size before terminating in the muscular tissue; and the nerve fibres generally are diminished or increased in diameter on passing into or out of the gray substance of the nervous centres. No absolute distinction therefore can be made between sensitive and motor fibres as regards their size; and in the essential details of their structure, namely, the tubular sheath, the medullary layer, and the axis cylinder, they are to all appearance completely identical.

Degeneration and Regeneration of Divided Nerves.—The immediate effect of dividing nerve fibres is to suspend their function. The communication between their extremities being cut off, the sensitive fibres can no longer transmit an impression from the skin to the nervous centre, and the motor fibres can no longer convey a stimulus of motion from the nervous centre to the muscles. This paralysis of motion and sensibility follows instantaneously upon the division of the nerve fibres.

But in addition to this result there also takes place, in the separated portion of the nerve, a structural degeneration of its fibres. The first indication of this change is visible in the medullary layer. It divides, in the course of each interannular segment, into two, three, or four distinct masses, the intervals between which are occupied, according to Ranvier,* by a new growth of nearly transparent, finely granular albuminous matter from the inner surface of the sheath of Schwann; which is already sufficient, in the rabbit, at the end of forty-eight hours, to fill at certain points the whole calibre of the sheath. The division of the medullary layer goes on until it is entirely broken up into globular masses of varying size, scattered irregularly through the substance of the fibre, and completely obscuring its normal structure. By this process, the continuity of the medullary layer is destroyed, its myeline being reduced to the condition of isolated oily-looking drops, and gradually transformed into a diffused granular mixture. Finally, the granules themselves disappear, and the tubular sheath, partially emptied by the atrophy of the medullary layer, becomes collapsed and wrinkled. Owing to the disappearance of the myeline, the nerve loses its white glistening aspect and assumes a grayish hue. According to the testimony of all recent observers, degeneration goes on at the same time in the axis cylinder. This portion of the fibre is enveloped and encroached upon by the growth of new matter, its continuity is broken at various points, its separated fragments are bent or folded upon themselves, and at last can no longer be made visible by the staining action of a carmine solution. Thus all the structural elements of the nerve fibre, excepting the sheath of Schwann, undergo a degeneration which results in complete atrophy.

The rapidity with which this change takes place varies with the species and age of the animal. It is less rapid in the cold-blooded, more so in the warm-blooded species. It goes on more quickly in the young, more slowly in full-grown animals. According to Vulpian, in young dogs, as a rule, the disappearance of the medullary layer is complete in six weeks or two months from the date of the injury.

The degeneration of the fibres of a divided nerve, whether sensitive

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* Histologie du Système Nerveux. Paris, 1878, tome i., p. 315.

or motor, extends throughout their entire length beyond the point of division to their peripheral terminations. Vulpian* found that in dogs, six weeks after division of the sciatic nerve, no unaltered nerve fibres could be discovered in the muscles of the corresponding foot. According to the same observer, the alteration is simultaneous, or nearly so, in all parts of the nerve beyond its division; being no further advanced near the point of section than toward the periphery. If there be any difference in this respect, the degeneration appears to be more rapid at the terminal extremity of the nerve; since, in the experiments of Ranvier, on the rabbit, forty-eight hours after division of the sciatic nerve, its terminal fibres in the muscles of the leg contained only separate masses of myeline in the form of oily drops.

The degeneration of divided nerve fibres involves the loss of their physiological properties. Immediately after the division of a motor nerve, the resulting paralysis is due only to its local discontinuity at the point of section, which arrests the passage of a nervous stimulus coming from the brain; and a galvanic current applied to the nerve below its division will still produce contraction in the muscles to which it is distributed. So long as this can be done, it shows that the nerve, though separated from the central parts, still retains its irritability, and is capable of responding to a stimulus by muscular action. But after a time this property disappears. In the rabbit, the irritability of a divided nerve is lost in forty-eight hours, in the pigeon at the end of three days, and in the dog at the end of four days; while in the frog it persists more or less for thirty days. These variations correspond with the rapidity of degeneration in the nerve fibres; and by comparative observations on different animals, Ranvier has shown that in all cases the disappearance of irritability of the nerve corresponds in time with the loss of continuity in the axis cylinder. This corroborates a conclusion derived from other sources, namely, that the axis cylinder is the essential element of the nerve fibre, through which its physiological action is transmitted.

A nerve, accordingly, some days after its division, has lost both its physiological properties and its anatomical structure. It can no longer convey sensitive impressions from the integument, and it is incapable of exciting muscular contraction. But this loss of function is not permanent. After a time the divided nerve may reunite, and its power of communication may be restored. This is shown, not only by the consolidation of its divided extremities and the reappearance of its normal physical aspect, but also by the reestablishment of its functions. The portions of integument which had lost their sensibility again become sensitive to external impressions, and the power of voluntary motion returns in the paralyzed muscles. This takes place by a regeneration of nerve fibres in the affected nerve beyond the point of division. All observers are now agreed that the nerve

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* Leçons sur la Physiologie du Système Nerveux. Paris, 1866, p. 243.

fibres thus produced are fibres of new formation. The old fibres have completely disappeared throughout the peripheral ramifications of the nerve, and their place is taken by others of subsequent growth.

The details of this regeneration are not fully known; but its essential characters, so far as they have been ascertained, are as follows: The new fibres begin to show themselves in the divided nerve before the complete disappearance of the old medullary granules. They are always smaller than the average size, and their interannular segments are shorter than in the fully developed condition; but in other respects their structure is normal, and even when very slender they exhibit annular constrictions, and a distinct medullary layer, capable of being stained by perosmic acid. They gradually increase in diameter, and in the thickness of their medullary layer; and when the process of regeneration is complete, the nerve again presents its normal whiteness and opacity.

There is some uncertainty as to the direction in which the growth of new fibres takes place. By several histologists it is maintained that the regenerated axis cylinders are offshoots from those in the central undegenerated extremity of the nerve; their growth extending thence into the peripheral portions. But this opinion is based only on analogy, from a similar growth of embryonic nerve fibres in the tail-membrane of the tadpole, and does not rest on any certain results of direct observation. It is possible that the new fibres may grow simultaneously throughout the separated portion of the nerve, increasing everywhere in development until their normal structure is attained. From numerous observations on this subject, it was the conclusion of Vulpian* that the regeneration of the fibres at any given time is the same at all points in the separated portion of a divided nerve. Vulpian and Philippeaux have also found that if the hypoglossal or the lingual nerve be divided, and the central portion extracted, so that no communication can be reëstablished with the nervous centres, the peripheral portion may be regenerated in the usual manner, notwithstanding its permanent separation from the central extremity. This would show that the power of regeneration resides in the nerve itself, the materials being supplied by the nutritive plasma of its own tissues.

The rapidity of regeneration in the fibres of a divided nerve, and the length of an excised portion which may be restored, vary with the age and species of the animal. According to Ranvier, after simple division of a nerve, in the rabbit, regeneration is in full progress at the end of nine or ten weeks, though many of the new fibres are of less than the average diameter. Vulpian found, in very young animals, a loss of nerve substance, from one to two centimetres in length, restored at the end of six weeks; and in young rats a portion of the sciatic nerve six millimetres long was reproduced in seventeen days. In adult animals, and especially in man, the restoration of divided nerves

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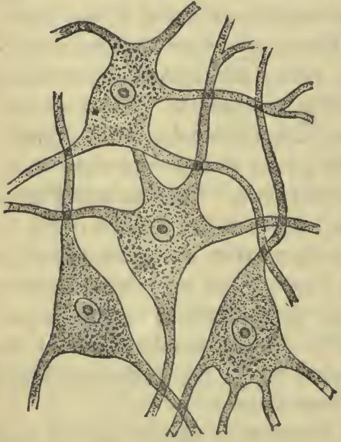
* Leçons sur la Physiologie du Système Nerveux. Paris, 1866, p. 258.

is much less rapid. When small nervous branches supplying the skin have been cut, the loss of tactile sensibility in the immediate neighborhood often persists for weeks or months after the healing of the wound. Restoration may sometimes take place in larger nerves, as in a case reported by L'Etiévant,* where the median nerve, in a man twenty-six years of age, was divided at the upper third of the arm. The power of motion and sensibility, in the parts supplied by this nerve, remained abolished for ten months, but began to reappear in fourteen months, and were nearly restored at the end of a year and a half. But according to both L'Etiévant and Mitchell,† when the injured nerves in man are of considerable size, the restoration of function, as a general rule, is either very imperfect or does not take place at all.

Nerve Cells.

The nerve cells, the characteristic anatomical element of the gray substance, are irregularly rounded bodies, consisting of a soft, nearly transparent, finely granular, albuminous matter, with a large, distinctly marked nucleus and nucleolus. They often contain in addition yellowish-brown pigment grains, imbedded in the substance of the cell. They vary in size in different regions. The smaller cells, from 10 to 20 mmm. in diameter, are found in the ganglia of the sympathetic system, parts of the cerebral hemispheres, and the posterior horns of gray matter in the spinal cord. The larger, from 40 to 60 mmm., are in the cerebellum and the medulla oblongata; and the largest of all are in the anterior horns of gray matter of the spinal cord, where they sometimes reach the diameter of 130 or 135 mmm., or seventeen times the size of the red globules of the blood.

FIG. 91.



NERVE CELLS, from the anterior horn of gray substance of the spinal cord.

The nerve cells are especially distinguished by their *processes*. These are narrow offshoots from the body of the cell, consisting apparently of the same finely granular albuminous material. Their number varies in different parts. In the Gasserian ganglion and the spinal ganglia of man, as well as in those of the dog, cat, rabbit, and frog, the nerve cells have each only a single process. In the sympathetic ganglia in man they have several; and in the gray substance of the brain, medulla oblongata, and spinal cord each cell presents from three or four to seven or eight processes, running in various

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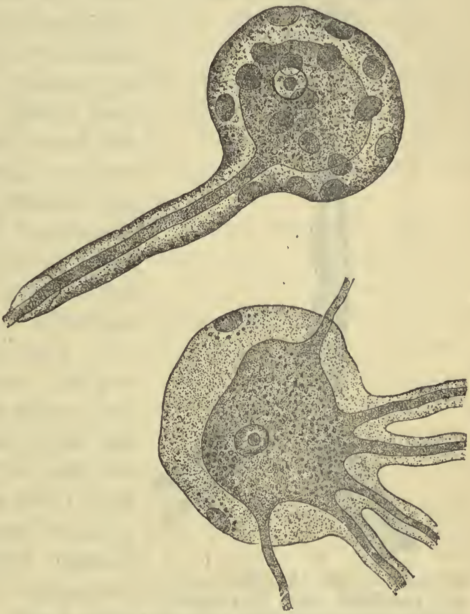
* Traité des Sections Nerveuses. Paris, 1873, p. 54.

† Injuries of Nerves, and their Consequences. Philadelphia, 1874, p. 84.

directions. At a certain distance from their origin, the processes are often branched, the branches again dividing and subdividing until reduced to a ramification of slender filaments. But in many instances, on the other hand, the cell-process extends for a considerable distance without division, as a nearly cylindrical or flattened filament, similar in appearance to the axis cylinder of a nerve fibre.

Each nerve cell, in its normal situation, is contained in a sheath or capsule, consisting of a thin, colorless, homogeneous membrane, with oval nuclei on its inner surface. In the fresh condition, the cell nearly fills the cavity of its capsule; but in preparations obtained with hardening fluids there is usually more or less shrinkage or condensation of the cell substance, so that it appears surrounded by a vacant space, limited by the inner surface of the capsule (Fig. 92). The cell-process, as it emerges, is accompanied by a tubular prolongation of the capsule, in which it lies enclosed.

FIG. 92.



NERVE CELLS, from spinal and sympathetic ganglia of man, enclosed in their capsular sheaths. From hardened preparations. (Key and Retzius.)

Connection between Nerve Fibres and Nerve Cells.—In all cases the nerve fibres are connected at their central origin with deposits of gray substance, into which they penetrate and in which they pursue an intricate course between its nerve cells. It is very difficult to distinguish the final connection of the two; since in the dilaceration of fresh specimens, both the fibres and the cell-processes are easily torn off; and in transparent sections of hardened specimens, a nerve fibre seldom follows the exact plane of the section for any considerable distance. But by a combination of both methods it has been shown that the nerve fibre is in many cases a continuation of the cell-process, and this continuity is so frequently visible that it may be regarded as the normal mode of connection between nerve fibres and nerve cells.

This connection is often extremely probable, in the spinal ganglia of man and mammalia, from the appearance of the cell-process, which soon after its origin resembles so completely an ordinary axis cylinder that there is no perceptible difference between them. It is rendered certain, according to the observations of Key and Retzius,* in the cerebro-spinal ganglia of the rabbit, where the cell-process follows for a time a winding course and becomes covered with a layer of myeline, which may be rendered perfectly distinct by staining with perosmic acid (Fig. 93). It thus forms a complete nerve fibre, often exhibiting its characteristic annular constrictions and incisions, and sometimes dividing into two secondary fibres.

Fig. 93.

Nerve Cell, with axis cylinder process and medullated nerve fibre attached; stained with perosmic acid. From Gasserian ganglion of the rabbit. (Key and Retzius.)

Some cell-processes, on the other hand, without acquiring a medullary layer, join nervous bundles in the neighborhood, and become to all appearance non-medullated nerve fibres. In all these instances the tubular prolongation, from the capsule of the nerve cell, is after a time closely applied to the exterior of the nerve fibre, becoming continuous with the sheath of Schwann.

A transition of the cell-process into a medullated nerve fibre has been also found in the spinal ganglia of the frog and toad, the layer of myeline reaching nearly to its junction with the nerve cell. But it is most distinctly marked, and has been most frequently seen in the ganglia and trunks of the trigeminus and vagus nerves of fishes, particularly the pike and lamprey. In these situations there are scattered nerve cells of peculiar form; namely, elongated or ovoidal, with a nerve process at each extremity. They are thence called "bipolar" cells. In the pike, the medullary layer surrounds the nerve fibre quite to its origin from the cell; and it sometimes extends over the cell itself, which, as well as the nerve fibre, is thus invested with a layer of myeline. These bipolar cells, as well as similar ones observed in the auditory nerve-trunk in fishes, sometimes appear hardly more than nucleated enlargements of the axis cylinder; and they are generally situated about midway between two annular constrictions. In the lamprey, the nerve fibres are non-medullated; but they are connected with bipolar cells in the ganglion of the trigeminus and in the trunk of the auditory nerve, in the same manner as above described.

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* Anatomie des Nervensystems und des Bindegewebes. Stockholm, 1876. Zweite Hälfte, p. 39.

These facts show beyond question the direct anatomical connection, in many instances, of the axis cylinder of nerve fibres with the processes of nerve cells. In the gray substance of the brain, medulla oblongata, and spinal cord, in man and mammalians, the multipolar nerve cells often present certain processes which assume the appearance of axis cylinders, and which join the bundles of fibres running in the direction of nerve roots. It is presumable, therefore, that they become after a time nerve fibres; although none of them, in these last named situations, have been seen invested with a medullary layer. According to Gerlach, on the other hand, there is a tract of gray substance in the spinal cord, throughout its dorsal portion, where the nerve cells, though provided with branching prolongations, do not present any process resembling an axis cylinder; and in the sympathetic ganglia of man, the dog, and the cat, Key and Retzius* have been able to follow the branched cell-processes for considerable distances among the neighboring tissues without ever seeing one of them converted into a medullated nerve fibre. It is possible that this may still have taken place beyond the point of observation; but it must also be considered as doubtful whether some nerve cells have not a different anatomical connection than that by cell-processes and axis cylinders.

Physiological Properties of the Nerve Cells.—The nerve cells, and the gray substance of which they form part, act as centres, in which nervous impressions are received through the sensitive fibres from the periphery, and from which a stimulus is sent out through the motor fibres to the muscles. Every such collection of gray substance is called a "nervous centre." While the nerve fibres accordingly are organs of transmission, the gray substance and its nerve cells are an apparatus in which the nervous influence is changed from one form to another. The nervous centre receives the impressions conveyed to it, and converts them into impulses to be transmitted elsewhere. How this change is effected in the nerve cells is unknown; but it is evidently essential to the physiological operation of the nervous system, since neither sensation nor movement is ever excited, in the normal condition, through the nerve fibres, unless they are in communication with a nervous centre.

In the action of the nervous system, therefore, the communication established between different parts of the body is always circuitous. It passes through a nervous centre, in which the impression coming from one organ is replaced by a stimulus which excites the other. This is called the "reflex action" of the nervous system, because it is first sent inward to the nervous centre and then returned or reflected in the opposite direction. In this process, the intermediate act between the inward and outward passage of the nervous current is accomplished in the gray substance.

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* Anatomie des Nervensystems und des Bindegewebes. Stockholm, 1876. Zweite Hälfte, pp. 125, 137.

CHAPTER II.

NERVOUS IRRITABILITY AND ITS MODE OF ACTION.

THE property possessed by nerves of being called into excitement by a stimulus is termed their "irritability." Such a property exists in other tissues and organs; and each one, when subjected to a stimulus adapted to its character, reacts in a way peculiar to itself, and produces a definite effect. Thus a gland, when excited, exhibits the phenomena of secretion; a muscle, those of contraction. The visible result of glandular activity is the accumulation and discharge of the secreted fluids; that of muscular contraction is a change of form in the muscle, and a movement of the parts to which it is attached. The irritability of a nerve, on the other hand, is not manifested by any perceptible change in its own tissue, but by the phenomena of sensation or motion in the organs to which it is distributed.

Irritability of Sensitive Fibres.

The irritability of sensitive nerve fibres is manifested by sensation. This sensation, however, is not felt in the nerve, but in the nervous centre where it terminates. For if the communication between a sensitive nerve and the brain be cut off, no stimulus subsequently applied to its trunk or branches will give rise to a sensation. But if this connection be retained, while that with the external integument is cut off, stimulants applied to the attached portion of the nerve will cause sensations more or less acute, according to the stimulus employed. Pinching or pricking the nerve, variations of temperature, or the passage of an electric current, will all bring into action its irritability, and thus produce a sensation.

For this result, however, two conditions are essential. First, the nerve must be, as above mentioned, in communication with its nervous centre; and secondly, the nerve fibres must retain their irritability. The irritability of a sensitive nerve may be so deadened by compression, contusion, or cold, that no stimulus applied to the part will produce a perceptible effect. In the observations of Mitchell,* the application of extreme cold, in man, to the region of the ulnar nerve at the elbow, produced, when the chilling process had reached a certain stage, complete loss of sensibility in the parts to which the nerve is distributed. The irritability of a sensitive nerve may also be suspended by injuries not involving its own fibres. Thus division of certain parts in the brain or spinal cord may produce a loss of sen-

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* Injuries of Nerves and their Consequences. Philadelphia, 1872, p. 59.

sibility in particular regions of the body, which disappears after a short time, while other symptoms, immediately dependent on the wound, are persistent;* and according to L'Etiévant,† section of one sensitive nerve may suspend, for a time, the sensibility of neighboring fibres derived from other nerves.

The irritability of sensitive nerve fibres may also be abnormally increased by vascular congestion or local injuries. The application of cold, or shutting off the supply of blood by the ligature of arteries, may produce in the nerve, before it reaches the stage of insensibility, a condition of unnatural excitement, indicated by pain in the parts corresponding to its distribution.

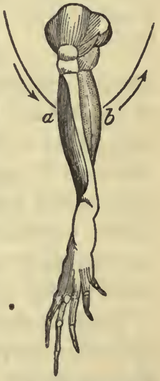
During life the irritability of sensitive nerves is manifested by conscious sensation. After death it may be shown to exist, for a certain time, by reflex actions taking place in the spinal cord and other parts of the nervous system.

Irritability of Motor Fibres.

The motor nerves are especially adapted for the study of nervous irritability, because their excitement produces a visible muscular contraction; and this may take place, after both the nerve and its muscle have been separated from the body. But to produce this result, as in the case of the sensitive nerves, two conditions are requisite, namely; first, the nerve fibres must preserve their irritability; and secondly, the muscle must be capable of responding to the nervous stimulus. These two conditions may therefore be studied in connection with each other.

Muscular Irritability.—This is best shown in the cold-blooded animals, in which it continues longer than in birds or mammalians. If a frog's leg be separated from the body, the skin removed, and the poles of a galvano-electric apparatus (Fig. 94, *a*, *b*) applied to the denuded muscles, a contraction takes place each time the circuit is completed. In this case, the electric stimulus acts directly on the muscles, and thus calls out their contractility. A single muscular fibre, placed under the microscope, may sometimes be seen to contract for a certain time after its separation from the neighboring parts. The muscles may also be excited by pinching, pricking, the contact of hot or cold bodies, or the application of acid, alkaline, or saline solutions. But the most efficient and manageable stimulus is the electric discharge.

Fig. 94.



Frog's Leg, with the poles of a galvanic battery applied to the muscles at *a*, *b*.

Nervous Irritability.—To exhibit the irritability of motor nerve fibres, a frog's leg is prepared, as in the preceding experiment, except that a portion of the sciatic nerve is retained in connection

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* Veyssière Recherches sur l'Hemianæsthésie. Paris, 1874, p. 78.

† Traité des Sections Nerveuses. Paris, 1873, pp. 171, 192.

with the amputated limb (Fig. 95). If the electrodes be now applied to the exposed nerve, and a current allowed to pass between them, at the moment of its passage a contraction takes place in the muscles below. In this case the electric current acts on the nerve alone: and the nerve excites the muscles by its own special agency. A muscular contraction, therefore, under the influence of a stimulus applied to the nerve, demonstrates the nervous irritability, and may be used as a convenient measure of its intensity.

Fig. 95.

Frog's Leg, with the sciatic nerve (N) attached, and the poles of a galvanic battery (*a*, *b*) applied to the nerve.

The irritability of a motor nerve continues after death. This follows from the foregoing experiment. The irritability of the nerve, like that of the muscles, depends upon its anatomical structure and constitution; and so long as these continue, the nerve retains its physiological properties. For the same reason, nervous irritability lasts longer after death in the cold-blooded than in the warm-blooded animals. Various artificial irritants may be employed to call it into activity. Pinching or pricking the exposed nerve with steel instruments, the application of caustic liquids, and the galvanic current, all have this effect. Galvanism, however, is the best means for this purpose, as it is more delicate in its operation than the others, and will succeed for a longer time.

Nervous irritability, like that of the muscles, is exhausted by repeated excitement. If an amputated frog's leg, with the sciatic nerve attached, be kept in a cool place, protected from desiccation, the nerve will remain irritable for many hours; but if excited by repeated stimulus, it soon begins to react with diminished energy, and at last ceases to exhibit any further irritability. If now allowed to remain at rest, its irritability will partially return; and muscular contraction will again ensue on the application of a stimulus to the nerve. Exhausted a second time, and a second time allowed to repose, the nerve will again recover itself; and this may be repeated several times in succession. At each repetition, however, the recovery of nervous irritability is less complete, until finally it can no longer be recalled.

Various circumstances tend to diminish or suspend the irritability of motor nerve fibres. As in the case of the sensitive fibres, compression, cold, or other similar agencies will depress the power of the muscular nerves, so that they can no longer excite contraction when subjected to the galvanic current. Severe and sudden mechanical injuries often have the same effect; as where general relaxation, or diminished power of voluntary motion, is produced, in man, by extensive contusion or laceration of the limbs. Such an injury produces a disturbance or *shock*, which affects the entire nervous system, and suspends its irritability; diminishing for the time both muscular power and sensibility. It is only after nervous irritability has been restored by repose, that voluntary motion and sensation are reëstablished.

Different Action of the Direct and Inverse Currents.—A galvanic current which traverses the nerve in the direction of its motor fibres, namely, from the centre toward the periphery, as from *a* to *b* (Fig. 95), is called a *direct* current. If made to pass in the contrary direction, from *b* to *a*, it is called an *inverse* current. When the nerve is exceedingly irritable, or with a galvanic current of considerable intensity, muscular contraction takes place at both the commencement and termination of the current, whether direct or inverse. But when the activity of the nerve has become somewhat diminished, or when the current employed is of feeble intensity, contraction takes place only at the *commencement* of *the direct* and at the *termination* of *the inverse* current. If both hind legs of a frog be prepared in such a way that they remain connected with each other by the sciatic nerves and a portion of the spinal column, when the positive pole of a battery is applied to the right foot and the negative pole to the left, the current passing through the sciatic nerves will be an inverse current for the right nerve, and a direct current for the left nerve. At the moment of completing the circuit, a contraction will take place in the left leg, but not in the right; and when the current is broken, the right leg contracts, while the left remains at rest. If the position of the poles be reversed, the effects of the current will be changed in a corresponding manner.

After a nerve has become exhausted by the direct current, it is still sensitive to the inverse; and after exhaustion by the inverse, it is still sensitive to the direct. It was even found by Matteucci that when a nerve has been temporarily exhausted by the direct current, the return of its irritability is hastened by the subsequent passage of the inverse current; so that it will become again sensitive to the direct current sooner than if allowed to remain at rest. Nothing, accordingly, is so exciting to a nerve as the passage of direct and inverse currents, following each other in quick succession. Such a form of galvanism is that afforded by the Faradic apparatus, in which rapidly alternating currents of induced electricity traverse the circuit in opposite directions.

The irritability of motor nerves is distinct from that of the muscles. This is shown by the fact that the two properties may be suspended independently of each other. In the experiment above described, the irritability of the nerve is manifested only through that of the muscle, and that of the muscle is called into action only through that of the nerve. But under the influence of *woorara*, the action of the motor nerve, as shown by Bernard,* may be suspended without affecting the irritability of the muscles. In a frog, poisoned by this substance, the poles of a galvanic battery applied to the sciatic nerve will produce no effect. But if the galvanic current be passed directly through the

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* Leçons sur la Physiologie du Système Nerveux. Paris, 1858, tome i., p. 199.

muscles of the leg, contraction takes place. The muscular irritability survives that of the nerves, and is therefore essentially distinct from it.

The independence of muscular and nervous irritability is also indicated by the effects following degeneration of divided nerve fibres (page 353). When a motor nerve is divided, the separated portion after a few days loses its irritability, so that no stimulus applied to it will excite contraction in the corresponding muscles. But if a galvanic current be applied to the muscles themselves, they contract. Longet* has demonstrated this fact upon the dog, from five days to twelve weeks after section of the facial nerve; and a similar result has been found by Vulpian† in the rabbit thirty days after section of the same nerve. The contraction in these cases cannot be attributed to the irritability of small nerve branches included in the muscular tissue, since the degeneration of a divided nerve takes place throughout its peripheral portion; and according to Ranvier‡, from forty-eight hours to five days after division of the sciatic nerve in the rabbit, the terminal nerve fibres in the muscles of the leg are as fully degenerated as those in the trunk of the nerve near its point of section. The irritability of the muscles must therefore be regarded as a property belonging to their own tissue, but capable of responding to a stimulus communicated by the nerves.

Identity of Action in Sensitive and Motor Fibres.

The results of nervous action are different in the two kinds of nerve fibres. The stimulation of sensitive fibres produces a sensation, or sensitive impression in the nervous centre; that of motor fibres causes muscular contraction at the periphery. Moreover, if a sensitive nerve be divided, stimulus applied to its central extremity still excites a sensation, while the same stimulus, applied to its peripheral portion, produces no apparent result. On the other hand, if a motor nerve be divided, irritation of its attached extremity, which is still in connection with the nervous centre, has no effect; but irritation of its peripheral portion causes muscular contraction as before. In other words, the nervous force, in a sensitive nerve, appears to move in a centripetal direction, that is from without inward; and in a motor nerve, in a centrifugal direction, or from within outward. The excitement of a sensitive nerve, furthermore, never produces any other immediate effect than a sensation; that of a motor nerve only gives rise to the phenomena of movement.

The above facts suggest the idea that the two kinds of nerve fibres may be distinct in their properties and modes of action; that the sensitive fibres may be capable of acting only in a centripetal direction and of exciting sensibility; and that the motor fibres can only act from

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* Traité de Physiologie. Paris, 1850, tome ii., p. 51.

† Leçons sur la Physiologie due Système Nerveux. Paris, 1866, p. 245.

‡ Leçons sur l'Histologie du Système Nerveux. Paris, 1878, tome ii., p. 349.

within outward, transmitting a special nerve force, adapted to excite muscular contraction.

It is evident, however, that these reasons do not indicate a real difference in the activity of the nerve fibres, but only in the sensible results of its operation. In neither case is there any perceptible effect produced in the nerve, but only in the organ with which it is connected. When a sensitive nerve is excited, the sensation is perceived in the nervous centre; when a motor nerve is called into activity, contraction takes place in the muscle. It is possible that the condition of the nerve under excitement may be the same in both cases, and that the difference in effect may be due only to the organ in which it terminates; just as the conducting wire of a galvanic battery may be made to ring a bell or move an index, according to the mechanism with which it is connected. There are some facts which can hardly bear any other interpretation than this, and which lead to the conclusion that the physiological action in the two kinds of nerve fibres is not essentially different.

1. *The stimulus applied to a nerve, either sensitive or motor, produces the same effect throughout its entire length.*

Impressions made upon the integument, which give rise to sensation, are transmitted by the sensitive nerve through its whole course to the nervous centre; and the sensation thus produced is referred, not to the brain or to any part of the nerve trunk, but to its point of distribution in the integument. An irritation applied to the same nerve in the middle of its course produces a sensation which still seems to come from the integument. After the amputation of a limb in man, if the severed extremity of a nerve be compressed or irritated in the cicatrix, the sensations excited are referred to the amputated limb; and patients often assert that they can feel the separated parts as distinctly as before. The impression conveyed through the remaining portion of the nerve is the same as if the whole of it were still in existence.

The motor nerves act in a similar way. A voluntary stimulus originating in the brain passes through the entire length of a motor nerve to reach the muscles and excite their contraction. If the nerve be divided at any intermediate point, and a galvanic stimulus applied to the peripheral portion, contraction follows in the muscles as before. In each case, the physiological effect is produced at the extremity of the nerve fibres; and is apparently of the same character, from whatever distance it has been transmitted.

It appears accordingly that the nerve fibre, whether sensitive or motor, when excited, is thrown into a condition of activity throughout its length; the nerve assuming a state of "polarity," analogous to that of a magnetized bar, in which the visible phenomena of attraction or repulsion are manifested only at its extremities, although the intermediate portions of the bar participate in its molecular action. When the exciting stimulus, in a sensitive nerve, is applied at the peripheral extremity, it must necessarily be transmitted from without inward; and when it commences at the inner extremity, as in a motor nerve, it must move from within outward. But under other conditions it may be capable of moving in either direction. The following experiment shows that this is possible, so far as regards the sensitive nerves.

2. *Sensitive impressions may pass, in the fibres of a sensitive nerve, either from without inward or from within outward.*

This of course never takes place in the normal condition; but its possibility has been demonstrated, in the experiments of Paul Bert,* by dividing a sensitive nerve and then reversing its position, so that its peripheral extremity is in connection with the nerve centres. The end of the tail, in a young rat, was deprived of integument for a length of five centimetres, and the denuded portion inserted beneath the skin of the back of the same animal. At the end of eight days, when the ingrafted portion had become adherent to the subcutaneous tissues, and had contracted sufficient vascular connection for its support, the tail was amputated at its base, and thenceforward remained attached to the body of the animal only by what was previously its peripheral extremity. In three months sensibility again began to be manifested in the end of the tail, thus reversed; and in six months it was reëstablished to an unmistakable degree. The nerves of the tail, which before the operation transmitted sensitive impressions from its point toward its base, afterward transmitted the same impressions from its base toward its point. In this instance the nerve fibres which thus acted in a reverse direction were fibres of new formation, like those which generally replace the degenerated fibres of divided nerves (page 355); but there is no evidence that such regenerated fibres are in any way different from those originally existing in the same parts.

Although the nerve fibres therefore may excite two different forms of action, their own condition may be the same for both. If they communicate their stimulus to a perceptive nervous centre the effect is a sensation; if to a muscle, it is contraction. These acts cannot be interchanged with each other, because the muscle is not sensitive and the nervous centre is not contractile; but they are both indirect effects of the nervous influence, and do not necessarily indicate any difference in its nature.

Rapidity of Transmission of the Nerve Force.

It is a matter of conscious experience that the operations of the nervous system require a certain time for their accomplishment. The action both of the senses and of the will, though exceedingly rapid, is not instantaneous. Between the mental decision to perform a movement and its actual execution, there is a short but real interval of time, during which the nervous mechanism is called into play. A certain period also intervenes between the contact of a foreign body with the skin, and our perception of its existence and qualities. There is even more or less difference between individuals in the time required

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* La Vitalité propre des Tissues animaux. Paris, 1866, p. 12.

for nervous action; the quickness of the senses and the promptitude of the will frequently varying to a perceptible degree. In the case of a voluntary movement, the period consumed is occupied by three different processes, namely: 1. The act of volition, in the brain; 2. The transmission of the motor impulse, through the spinal cord and nerves, to its destination; and 3. The excitement of the muscle to contraction. In the case of a sensation, there are three analogous successive acts, namely: 1. Reception of the impression by the sensitive membrane; 2. Transmission of the stimulus through the nerve toward the brain; and 3. Its perception in the brain as a conscious sensation. It is important to determine the rapidity of nervous communication in each direction.

Methods of Determining the Rate of Transmission of the Nerve Force.—The rate of transmission of the nerve force, first measured by Helmholtz,* has since been investigated by different observers with essentially similar results. The principle adopted is in all cases the same. Muscular contraction is excited by a stimulus which passes through two nerves of different length, or through two different lengths of the same nerve; the delay in contraction, when the stimulus passes through the longer of these routes, gives the time required to traverse the additional distance.

These experiments were first performed on separated nerves and muscles of the cold-blooded animals. The gastrocnemius muscle of a frog is prepared, with a portion of the sciatic nerve attached. A galvanic battery with an induction apparatus is also provided, so that the closure of the battery circuit will produce an instantaneous current in the induction coil. This induced current is first applied to the muscle, and the time noted which intervenes between the closure of the circuit and the muscular contraction. This represents the period required for the excitement of the muscular fibres, and was found by Helmholtz to be about $\frac{1}{100}$ of a second. If the stimulus be now applied to the nerve near its termination in the muscle, the interval is not perceptibly changed. But if it be applied at a point one, two, or three centimetres distant, a retardation is manifested in the muscular contraction; and this retardation becomes greater as the distance between the muscle and the point of stimulation is increased.

The intervals of time in these experiments have been measured by various contrivances, the most successful of which is an automatic registering apparatus like that of Marey (page 284). Upon the surface of the revolving cylinder the extremity of a tuning-fork, vibrating 500 times per second, traces an undulating line (Fig. 96, *a*) which records the time occupied in moving from one point to another. A straight horizontal line (*b*) is also traced upon the same surface by the extremity of a slender lever, the other end of which forms part of the galvanic circuit. The closure of the circuit is accomplished by a movement

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* Comptes Rendus de l'Académie des Sciences. Paris, 1851, tome xxxiii., p. 262.

which pushes aside the lever, causing in the traced line a momentary deviation (*d*), which thus registers the instant of the stimulation of the nerve. The muscle used for experiment is attached by its tendon to a second lever in such a way that any muscular contraction will draw aside its free extremity. This lever, while at rest, traces a second horizontal line (*c*) below the first; and when the muscle contracts, the line is deviated, as at (*e*), by the movement of the lever.

FIG. 96.

DIAGRAM OF THE REGISTERING APPARATUS, according to the plan of Marey. *a.* Undulating line traced by the tuning-fork, which marks the time consumed by the card in moving from one point to another. *b.* Line traced by the first lever, forming part of the galvanic circuit. *c.* Line traced by the second lever, which is moved by the contraction of the muscle. *d.* Deviation of the line *b*, indicating the closure of the galvanic circuit and the stimulation of the nerve. *e.* Deviation of the line *c*, indicating the muscular contraction.

There are thus left upon the registering surface two deviations, *d* and *e*, one of which records the stimulation of the nerve, the other the muscular contraction; and between the two there is a certain interval. The number of undulations in the trace *a*, corresponding to this interval, indicates the time which has elapsed between the stimulation of the nerve and the muscular contraction. In the example shown at Fig. 96, as the interval between the deviations includes 13 simple vibrations, of which 500 would represent one second, the time occupied is 0.026 of a second. By this means, intervals of very short duration may be accurately registered.

Subsequently investigations of a similar kind were applied to the man during life. In the experiments of Baxt,* this was done by applying electrodes to the skin over the median nerve, at varying distances from its muscular distribution. The nerve was thus stimulated at the wrist, at the elbow, and at the upper arm; the effect being marked by the swelling of the muscles at the ball of the thumb. The time intervening between the application of the electrodes and the muscular contraction was greater with the stimulus applied at the upper arm, than at the wrist; the difference being evidently the time required to transmit of the nervous impulse from the first point to the second. The rate of transmission, as ascertained by these experiments, varied according to the conditions of cold or warmth; being less rapid at a low than at a high temperature.

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* Monatsbericht der königlichen Preussischen Akademie, 1867 and 1870.

Finally, the rate of transmission of the nerve-force, in man, for both voluntary motion and conscious sensation, has been investigated by Burckhardt,* with a registering apparatus in which the beginning and end of the nervous transmission were marked, as above, by the deviations of a traced line.

Rate of Transmission in the Motor Nerves.—The transmission of the voluntary impulse was measured by Burckhardt as follows: The apparatus being attached to the person serving for experiment, the signal for voluntary motion was given by a bell connected with the battery. Thus the entire interval registered was that between the sound of the bell and the muscular contraction. A part of this time was consumed in hearing the sound and producing the volitional impulse. Another part was taken up by the process of muscular contraction; and only the remainder was occupied by nervous transmission. But when, in different observations, the same signal was used for the contraction of muscles supplied by different lengths of nerve, the processes taking place in the brain and in the muscle would be alike in all; and any difference in the time observed must be due to the different lengths of nerve traversed by the motor impulse. The muscles employed for this purpose were, in the lower limb, the extensor digitorum communis brevis, tibialis anticus, and semimembranosus, supplied by branches of the sciatic nerve, and the quadriceps extensor cruris, supplied by the anterior crural nerve; in the upper limb, the interosseus externus primus, extensor digitorum communis, flexor digitorum and deltoid, all supplied by branches of the brachial plexus. The mean result of these observations, on eight healthy persons, gave a velocity of transmission, in the nerves of the upper and lower limbs, of a little over 27 metres per second. The minimum velocity was 20 metres, and the maximum 36 metres; but of all the observations, thirty in number, twenty-three, or nearly four-fifths, gave results between 26 and 28 metres.

In one instance the rate of movement for the voluntary impulse and for that excited by galvanism was tested in the same nerve, with but little difference in the results.

According to Burckhardt, furthermore, the rate of transmission does not vary essentially for weak or strong motor impulses; that for a muscular contraction of moderate force passing as rapidly through the nerve as that for contractions of greater power.

Rate of Transmission in the Sensitive Nerves.—The rate of transmission for impressions of conscious sensibility is determined by a similar method. A tactile impression is made upon the skin at varying distances from the nervous centre—as, for instance, upon the foot, the thigh, and the loins; the instant at which the sensation is perceived being indicated by a movement of the finger. As the time required for conscious perception in the brain and for voluntary movement of

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* Die Physiologische Diagnostik der Nervenkranheiten. Leipzig, 1875, p. 32.

the finger is the same in all cases, the difference between successive observations is due to the different lengths of nerve transmitting the impression.

In the experiments of Burckhardt, made on thirteen different persons, the mean rate of transmission for sensitive impressions through the nerves was a little less than 47 metres per second; that is, more than one and a half times as rapid as that for voluntary motion. The variations were from a minimum of 20 to a maximum of 73 metres; but in nearly three-fourths of all the observations, the results were confined within the limits of 40 and 56 metres. The rapidity of transmission varied but little with the intensity of the impression; the difference, on the average, being but little over one per cent. The average rate for different kinds of nervous action is accordingly as follows:

Rate of Transmission through the Nerves.

For voluntary motion	27 metres per second.
For sensation	47 " " "

Rate of Transmission in the Spinal Cord.—The investigations of Burckhardt first indicated a difference between the rate of transmission in the spinal cord and that in the nerves. This rate was determined for the spinal cord by comparing the passage of a voluntary impulse through two nerves, like the sciatic and the ulnar, which emerge from the spinal cord at different points. In this case the impulse, after leaving the brain, traverses different lengths of the spinal cord; and as its rate of movement in the peripheral nerves is known, the difference in time of its entire passage gives its rate of movement in the spinal cord. Thus a motor impulse, which calls into action the interosseous muscles of the hand, passes through the cervical portion of the spinal cord, the lower cervical nerves, the brachial plexus, and the ulnar nerve. An impulse which excites contraction in the quadriceps extensor cruris passes through the cervical and dorsal portions of the cord, and thence through the lumbar plexus and the anterior crural nerve to the thigh. Consequently its transit through the spinal cord is about three times as long in the second case as in the first; and the amount of its retardation must correspond with this difference.

By this means it was found that the transmission of *voluntary motor impulses* in the spinal cord is considerably slower than in the nerves. Its average rapidity was a little over 10 metres per second; the minimum being 8, the maximum 14 metres. Thus the difference in rapidity of transmission through the nerves and the spinal cord is very manifest.

A comparison of the opposite sides of the body gave a difference in the rate of transmission, for the right and left halves of the spinal cord, of from one to three metres per second, always in favor of the left side.

The transmission of *sensitive impressions* through the spinal cord, on the other hand, was found to be nearly as rapid as through the nerves, the average rate being a little over 42 metres per second. There was a remarkable difference, however, in this respect, between tactile impressions and those of a painful character. The latter are transmitted at a much slower rate, amounting on the average to not more than 13 metres per second. Thus the transmission of motor impulses and of tactile and painful impressions respectively, through the spinal cord, is as follows:

RATE OF TRANSMISSION THROUGH THE SPINAL CORD.

For tactile impressions	42 metres per second.
" painful	13 " " "
" motor impulses	10 " " "

According to these results the passage of a motor impulse, from the brain to the muscles of the foot, would occupy 0.088 of a second; of which about one-half would be required for transmission through the spinal cord, and one-half for transmission through the nerves.

Rapidity of Nervous Action in the Brain.—In the above experiments, an essential part of the nervous operation consists in hearing the signal for a voluntary movement and in the volition which generates the motor impulse. The time thus consumed is ascertained by deducting, from the whole period between a given signal and a voluntary movement, first, the time requisite for muscular contraction, namely, 0.01″; and, secondly, that occupied in transmitting the impulse through the spinal cord and nerves. Thus if the entire period be 0.220″, and the time required for transmission through the spinal cord and nerves be 0.088″, there remains 0.132″, which is occupied in muscular contraction and in the acts of sensation and volition. Burckhardt's experiments, like those of Helmholtz, fix the time required for local stimulation of the muscle at 0.01″; and he estimates that about an equal interval is necessary for the mechanism of hearing. The whole process, therefore, of executing a voluntary movement in the foot, at the signal of a bell, would be divided as follows:

TIME OCCUPIED IN EXECUTING A VOLUNTARY MOVEMENT AT A GIVEN SIGNAL.

Mechanism of hearing	0.010″
Acts of perception and volition in the brain	0.112″
Transmission through the spinal cord	0.044″
Transmission through the sciatic nerve	0.044″
Mechanism of muscular contraction	0.010″
	0.220″

It appears that the action in the brain, representing the operation of the gray substance of the nervous centres, requires a considerably longer time than the transmission of impulses through the nerve fibres.

Personal Error and Personal Equation.—The different rapidity of nervous action, in different individuals, causes a variation in the promptitude with which they perceive and record sensible phenomena. This was first noticed in astronomical observatories, where it was found that the passage of a star across the thread of a transit instrument was differently recorded by different observers; the difference sometimes amounting to as much as one second. Subsequent observations showed that in no case was the time recorded with absolute accuracy; but that a certain delay always intervened, due to the time occupied by the nervous mechanism of the observer. This fact was established by imitating the transit of a star by means of a luminous point moving with uniform velocity before the field of a telescope. By contrivances like those above described, the real instant of the passage of the luminous point across the thread of the telescope is recorded upon a revolving cylinder, and the observer also marks its passage by similar means. The difference between the real and the observed time represents the "personal error" of the observer. As it is important to eliminate this error from the record of astronomical observations, when its amount has been determined for any particular observer, his record is corrected by a corresponding quantity. This is termed the "personal equation" of the observer.

The error of any particular individual remains nearly the same, as compared with that of other persons; that is, it will be habitually greater or less in one observer than in another. But, like all physiological peculiarities, it varies somewhat in the same individual; and according to Kampf,* it may change perceptibly even in one night. The following table shows the varying personal equation of two different observers in fractions of a second, as ascertained on three successive days:

ABSOLUTE PERSONAL EQUATION OF

	Lieut. Tillman.	Dr. Kampf.
May 1	—0.125	—0.027
May 2	—0.121	—0.021
May 3	—0.116	—0.026

Where extreme accuracy is required, as in observations for longitude, it is consequently recommended by Dr. Kampf that the personal error of the observer be determined and corrected at the time of each observation.

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* On the Determination of Personal Equations. Report upon United States Geological Surveys west of the One Hundredth Meridian. Washington, 1877, p. 475.

CHAPTER III.

GENERAL ARRANGEMENT OF THE NERVOUS SYSTEM.

THE nervous system, in man and the higher animals, includes two secondary systems, or groups of nervous centres, with their commissural fibres and peripheral nerves. They are: first, the cerebro-spinal system, presiding over the functions of animal life; and, secondly, the sympathetic system, connected with the internal acts of nutrition.

Cerebro-Spinal System.—Of the two groups above mentioned, the cerebro-spinal system largely preponderates by its mass, the well-marked distinction of its parts, and the striking character of its phenomena. Its centres are also, in great measure, the sources of functional activity for the sympathetic system, and thus control, directly or indirectly, the nervous relations of the whole body. As its name indicates, the nervous centres belonging to it are the brain and the spinal cord; the nerves which originate from them being distributed to the muscles and tegumentary surfaces of the head, trunk, and limbs, to the organs of special sense, and to the commencement and termination of the internal passages of the body.

In its general form the cerebro-spinal system is distinguished by a nearly complete bilateral symmetry. Like the organs of animal life over which it presides, it consists of a double series of corresponding structures, united with each other upon the median line. This union is effected by transverse *commissures;* that is, by fibrous tracts passing from side to side between similar parts and enabling them to act in harmony with each other. The right and left halves of the brain and spinal cord, thus connected, furnish the nerves of sensation and motion to the two sides of the body.

Another peculiarity of this portion of the nervous system is the *decussation* of its fibres. By this term is meant an oblique passage of fibres across the median line, forming a connection between dissimilar parts on the two sides; and as this oblique crossing takes place simultaneously from right to left and from left to right, the two tracts of decussating fibres are interwoven with each other at the median line. This is most distinctly shown in the decussation of the optic nerves at the base of the brain and in that of the anterior pyramids at the medulla oblongata; but other instances occur at various points in the interior, and it may be said, in general, that the nerves emerging from the right side of the cerebro-spinal mass have their origin in the gray substance of the left side, and those emerging from the left side have their origin on the right. The only uncertainty in this respect is whether the decussation be complete or partial; that is, whether all the fibres of a given nerve root be connected with the opposite side of the central mass, or whether a part of them originate from the same, and a part from the opposite side. In a large number of instances the decussation is anatomically demonstrated; in others it is inferred from the results of experiment. But there can be no doubt that it is a general feature in the arrangement of the cerebro-spinal system.

The *spinal cord* is the simplest and most fundamental part of this system. It is a nearly cylindrical nervous mass, extending from its junction with the brain above to its inferior termination at the level of the second lumbar vertebra. A transverse section shows that it is incompletely divided into right and left lateral halves by anterior and posterior median fissures; of which the anterior is the wider and shallower, while the posterior is narrower and deeper. The interior of the cord consists of gray substance, in the form of a double crescentic-shaped mass, with the concavities of the crescents turned outward. As these masses are found at all parts of the cord, they are in reality elongated bands of gray substance, one on each side of the cord, running continuously throughout its length. They are united with each other by a transverse band of gray substance, containing nerve fibres, and known as the "gray commissure," in the centre of which is a narrow longitudinal canal, the "central canal," about 0.2 millimetre in diameter, lined with epithelium.

Fig. 97.

Transverse Section of the Spinal Cord.—*a*, *b*. Spinal nerves of right and left sides. *d*. Origin of anterior root. *e*. Origin of posterior root. *c*. Ganglion of posterior root.

The anterior and posterior portions of gray substance, in each lateral half of the cord, are called the anterior and posterior *horns*. Immediately in front of the gray commissure is a band of white substance, the "white commissure" of the cord.

The spinal nerves are given off from the cord at regular intervals in symmetrical pairs; and are distributed to the integument and muscles of the corresponding regions. In fish and serpents, where locomotion is performed by lateral flexion of the spinal column, the cord is nearly uniform in size, or tapers gradually to its posterior extremity. But in birds and quadrupeds, where there are special organs of locomotion, as fore and hind legs, or legs and wings, the cord is increased in size where the nerves of these organs are given off. In man, the lower cervical nerves which supply the arms, and the sacral nerves which supply the legs, are larger than those given off in other regions; and the cord itself presents two enlargements corresponding with the origin of these nerves, namely, the *cervical enlargement*, which is the source of the nerves for the upper limb, and the *lumbar enlargement*, which gives off the nerves for the lower limb.

The origin of the spinal nerves on each side of the cord is by two sets of fibres, forming anterior and posterior roots. The anterior root (Fig. 97, *d*) emerges from the cord opposite the anterior horn of gray matter. The posterior root (*e*) originates at a point corresponding with the posterior horn of gray matter. Both roots are composed of numerous fibres, united in parallel bundles. The posterior root is distinguished from the anterior by the presence of a small rounded mass of gray matter, or ganglion, beyond which the two roots unite in a common trunk.

The white substance of each lateral half of the cord is thus divided into three portions or "columns;" so called because the nerve fibres composing them run, for the most part, in a longitudinal direction. The portion included between the anterior median fissure and the anterior nerve roots is the *anterior column;* that between the anterior and posterior nerve roots is the *lateral column;* while that between the posterior nerve roots and the posterior median fissure is the *posterior column.* As the posterior median fissure penetrates the cord quite to the gray commissure, the posterior columns appear entirely separated from each other in a transverse section; while the anterior columns are connected by the white commissure above mentioned.

The *brain*, or "encephalon," is that portion of the cerebro-spinal mass contained in the cranial cavity. It consists of various deposits of gray substance, connected with each other and with the spinal cord by transverse, oblique, and longitudinal tracts of nerve fibres. The number and size of its nervous centres vary in different animals according to their general bodily organization, and the special development of their nervous functions.

Fig. 98.

Brain of Alligator.—1. Olfactory Ganglia. 2. Hemispheres. 3. Optic Tubercles. 4. Cerebellum. 5. Medulla Oblongata.

In *fish* and *reptiles* the nervous centres of the brain are so distinctly separated, and of such moderate size, that they are often designated as "ganglia." In the alligator (Fig. 98) there are five pairs of these ganglia, arranged in a double linear series. The first are the *olfactory ganglia* ($_{1,1}$) which distribute their nerves to the olfactory membrane, and are connected with the rest of the brain by slender longitudinal tracts of white substance. The next pair ($_{2,2}$), somewhat larger and of triangular shape, are the "hemispherical ganglia," corresponding to the *hemispheres*, or cerebrum in the higher classes. Immediately following them are two quadrangular masses ($_{3,3}$) which give origin to the optic nerves, and are therefore called the *optic ganglia;* but in some of the higher animals, where they are imperfectly divided into four nearly equal parts, they are known as the "tubercula quadrigemina." Behind them is a triangular collection of nervous matter ($_4$), the *cerebellum.* Finally, the upper portion of the cord, just behind and beneath the cerebellum, is enlarged into a double oblong mass ($_{5,5}$), the *medulla oblongata.*

In *birds* the cerebrum is comparatively larger, and nearly or quite conceals the optic tubercles in a view taken from above. The cerebellum is well developed, and presents on its surface a number of transverse foldings or convolutions by which its gray substance is increased in quantity; and it extends so far backward as to completely cover the medulla oblongata.

Fig. 99.

Brain of Pigeon.—Profile View.—1. Cerebrum. 2. Optic Tubercle. 3. Cerebellum. 4. Optic Nerve. 5. Medulla Oblongata.

In *quadrupeds*, the cerebrum attains a still greater size, as compared with remaining parts of the brain, and in the more highly developed orders it is so much increased as partly to cover the olfactory ganglia in front and the cerebellum behind; its surface at the same time presenting numerous convolutions. It also contains near its base, on each side the median line, two additional collections of gray substance; namely, the "corpora striata" and "optic thalami." These bodies are often designated as the "cerebral ganglia," since they occupy the inferior parts of the cerebrum, and receive the tracts of white substance entering it from below. The cerebellum in quadrupeds is enlarged by the development of its lateral lobes, and is marked by abundant transverse convolutions.

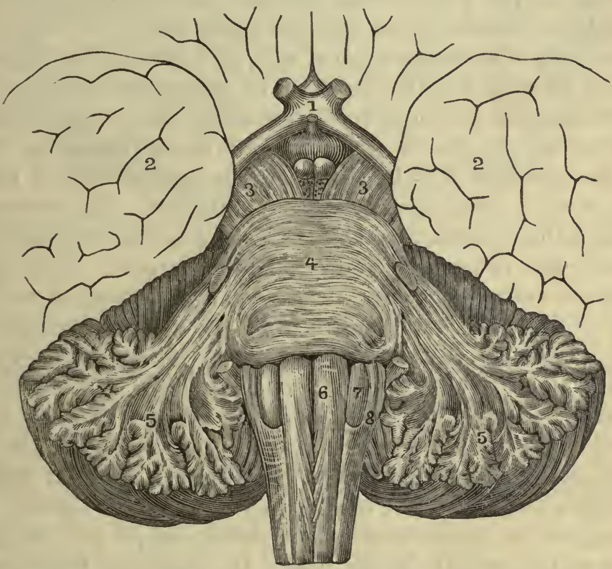
In *man* the cerebrum reaches its highest development, and preponderates completely over all the remaining nervous centres. In the human brain, accordingly, when viewed from above, there is nothing to be seen but the convoluted surface of the hemispheres; and even in a posterior view they cover everything but a portion of the cerebellum. The remaining parts, however, although concealed by the cerebrum and cerebellum, participate in the structure of the encephalon, forming, as in the lower animals, a series of associated nervous centres, with connecting tracts of nerve fibres.

As the spinal cord enters the cranial cavity, it enlarges to form the medulla oblongata. This portion of the cerebro-spinal axis is distinguished from the cord below, not only by its form, but also by the arrangement of its gray and white substance. The gray substance, which in the cord presents on each side the projections of the anterior and posterior horns, recedes, in the medulla oblongata, in a backward direction, expanding into a continuous layer at its posterior surface.

At the same time, the posterior columns of white substance diverge at an acute angle, leaving between them the fourth ventricle, and, under the name of the *restiform bodies*, become continuous with the inferior peduncles of the cerebellum.

In front, the medulla oblongata presents two longitudinal eminences of white substance, one on each side of the median line, the *anterior pyramids*, which take the place of the anterior columns of the cord. At their lower portion they exhibit the well-known *decussation*, formed by oblique bundles of fibres crossing the median line from below upward and from side to side. Thus the right anterior pyramid is formed of fibres which come from the left side of the cord, and the left anterior pyramid of those which come from the right side of the cord.

FIG. 100.



MEDULLA OBLONGATA AND BASE OF THE BRAIN IN MAN.—1. Decussation of the Optic Nerves. 2, 2. Middle Lobes of the Cerebrum. 3, 3. Crura Cerebri. 4. Tuber Annulare. 5, 5. Lateral Lobes of the Cerebellum. 6. Anterior Pyramid. 7. Olivary Body. 8. Restiform Body. (Hirschfeld.)

Immediately outside the pyramids are two elongated oval masses, the *olivary bodies*, which consist externally of white substance, but internally contain a thin convoluted layer of gray substance, resembling in miniature the convolutions of the hemispheres. They are special deposits of gray substance in the medulla oblongata, superadded to the rest, and not continuous with that of the spinal cord.

At the upper limit of the medulla oblongata is the *tuber annulare*, so called because it forms a ring-like protuberance at the base of the brain. Superficially, it consists of transverse bundles of fibres passing over, in an arched form, from one side of the cerebellum to the other. Where they cross the tuber annulare these fibres constitute the "pons Varolii;"

at the sides, where they turn backward, they form the "middle peduncles of the cerebellum."

In its deeper parts, the tuber annulare contains longitudinal tracts of white substance, passing upward from the medulla oblongata toward the cerebrum. The continuation of the anterior pyramids in front, and the remaining longitudinal bundles of the medulla oblongata behind, pass into and through the tuber annulare, between various irregularly diffused deposits of gray substance. From the upper border of the tuber annulare, they emerge in the form of two obliquely diverging bundles of nerve fibres, the *crura cerebri,* or peduncles of the brain. They are joined posteriorly by other longitudinal bundles coming from the cerebellum, known as the "anterior peduncles of the cerebellum," and forming the tracts of communication between the cerebellum and the cerebrum. The crura cerebri then pass into the base of the brain, thus completing its connection with the spinal cord.

The structure of the cerebro-spinal axis, as a whole, may be described as follows: There is a continuous tract of gray substance, surrounding the central canal of the spinal cord, expanding into a superficial layer on the floor of the fourth ventricle, and thence extending forward around the aqueduct of Sylvius and on the vertical sides of the third ventricle, until it terminates at the infundibulum. This is the "gray substance of the medullary canal," and from it all the nerves of voluntary motion and general sensibility take their origin. Near its upper part there are various additional deposits of gray substance, the largest of which is the cerebellum; and beyond its upper extremity is the cerebrum, containing the cerebral ganglia at its base, and expanding above into the convolutions of the hemispheres. The two hemispheres are connected with each other by a broad transverse commissure of white substance, the "corpus callosum," covering the lateral ventricles and the cerebral ganglia; and the two lateral halves of the cerebellum are united in a similar way by the pons Varolii.

The longitudinal connections of the cerebro-spinal axis are the continuations of the columns of the cord. On emerging from the tuber annulare, under the form of the crura cerebri, they enter the base of the brain, and meet at once with the gray substance of the cerebral ganglia. They pass through and between these ganglia, forming in this situation the so-called "internal capsule;" and from its upper border they spread out on each side into an expanding crown of divergent fibres, known as the "corona radiata." The fibres of the corona radiata thence disperse in every direction, to reach, at last, the gray matter of the cerebral convolutions.

It is by no means certain that the individual nerve fibres are continuous throughout these longitudinal connections. On the contrary, the study of successive microscopic sections, by the best observers, has failed to show such a direct continuity; and it is considered more probable that the fibres coming from one portion of the cerebro-spinal axis terminate in certain deposits of gray substance, and that the connection is continued by new fibres originating from the same or adjacent cells. According to this view, the longitudinal tracts consist of fibres which are interrupted in their course by different deposits of gray substance; so that an impression or impulse conveyed from one region to another is not the same throughout, but is modified in character by the nervous centres which successively receive and transmit it. How many such interruptions there may be in the transmission of nervous impulses is not known; but it must be considered that, for ordinary motor and sensitive acts, there are, counting from without inward, three successive nervous centres through which they pass; namely,

Fig. 101.

Diagram of Human Brain in Transverse Vertical Section.—1. Tuber Annulare; 2, 2. Crura Cerebri. 3, 3. Internal Capsule. 4, 4. Corona Radiata. 5, 6. Cerebral Ganglia. 7. Corpus Callosum.

1st. The gray substance of the medullary canal;

2d. The cerebral ganglia at the base of the brain; and

3d. The convolutions of the hemispheres.

There are also three sets of fibres in the longitudinal connecting tracts:

1st. The nerves and nerve roots, connecting the peripheral organs with the gray substance of the medullary canal;

2d. The columns of the cord and the crura cerebri, connecting the gray substance of the medullary canal with the cerebral ganglia; and

3d. The fibres of the corona radiata, connecting the cerebral ganglia with the convolutions of the hemispheres.

Thus between the cerebral convolutions and the peripheral organs are two intermediate stations of nervous matter; namely, the cerebral ganglia and the gray substance of the medullary canal; and when a nervous impulse passes from the cerebral convolutions to the peripheral organs, or *vice versâ,* three successive sets of nerve fibres take part in its transmission.

In each separate region of the cerebro-spinal system, furthermore, the gray substance may act as a nervous centre, to transform sensitive impressions into a motor impulse, and thus give rise to reflex action. Such a reflex action may take place in the nervous centre nearest the periphery, without calling into operation any other than its own special endowments, and without presenting any character of consciousness or volition. But the sensitive impression may also be transmitted through the whole series of longitudinal connections to the cortex of the brain; and the motor impulse thus excited may pass in the reverse direction through its entire route to the muscles of the limbs. The convoluted layer of gray substance in the cerebral hemispheres serves therefore as a great concave mirror, by which impressions coming from without are received as conscious sensations and ideas, and reflected in the form of intelligent, voluntary acts. To produce this result, the whole mechanism of the cerebro-spinal system is called into operation, each part acting in succession, to modify or transmit the nervous impulse.

CHAPTER IV.

THE SPINAL CORD.

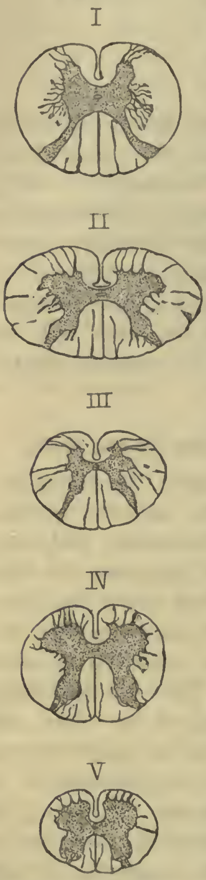
THE spinal cord is that part of the cerebro-spinal system contained in the spinal canal, and which sends its nerves to the muscles and integument of the trunk and limbs. It consists externally of white substance, forming longitudinal tracts of nerve fibres, the continuations of which make connection with the brain above; and internally of gray substance surrounding its central canal, and occupying the interior of its lateral halves. It is therefore constituted to act in a double capacity: First, as a medium of communication between the brain and the peripheral organs; and secondly, as an independent nervous centre, with special endowments of its own.

Arrangement of Gray and White Substance in the Spinal Cord.

The relations of the gray and white substance form the necessary basis for a physiological anatomy of this part of the nervous system. The connections of the nerve fibres with the gray substance, and their course in the longitudinal columns, are the most important for this purpose. These relations are not fully known; but much has been accomplished in this respect by the examination of transverse and longitudinal sections of the cord, either in the fresh condition or after the use of hardening and staining preparations. The size and form of the cord, as well the quantity and configuration of its white and gray substance, vary much in its different parts. In the upper cervical region, it is nearly cylindrical; at the cervical enlargement, it is widened laterally, and flattened in an antero-posterior direction; in the dorsal region, it again approximates the cylindrical form, but is reduced in size; its second enlargement is at the beginning of the lumbar region; after which it diminishes rapidly to its termination. It is evident from an inspection of its section surfaces at different levels, that the cervical and lumbar enlargements are mainly due to an increased quantity of gray substance in these regions; and that the white substance, on the whole, diminishes gradually from above downward. This agrees with the double physiological character of the cord; its gray substance acting as a nervous centre for the corresponding regions of the body, while its white substance, at any one point, represents the tracts of communication for nerves given off below.

The Gray Substance.—The gray substance in the spinal cord, as elsewhere, is a mixture of nerve cells and nerve fibres, of which the nerve cells are the distinctive element. They are all provided with cell processes running in various directions, most of them exhibiting abundant ramifications, while some continue their course for a considerable distance undivided, and assume at last the appearance of axis cylinders. The largest and most remarkable are situated in the anterior horns, where they reach the size of from 67 to 135 mmm. in diameter; many of them being the largest known cells in the nervous system. They are mainly arranged on each side in three groups, namely, at the point, and at the external and internal borders of the anterior horn. Throughout the dorsal region there is a group of similar cells at the base of each posterior horn, known as the "column of Clarke," extending from the lower cervical region nearly to the lumbar enlargement. Here these cells disappear as a distinct group, while those of the anterior horns increase considerably both in numbers and size. Elsewhere throughout the gray substance, but especially in the posterior horns, the nerve cells are much smaller, but similar in form, and provided with branching prolongations. The anterior and posterior horns are not therefore absolutely distinguished from each other by the size of their nerve cells, but only by the relative abundance of the larger and smaller varieties; since a few large cells are found in the posterior horns, and the smaller cells exist in both regions.

Fig. 102.

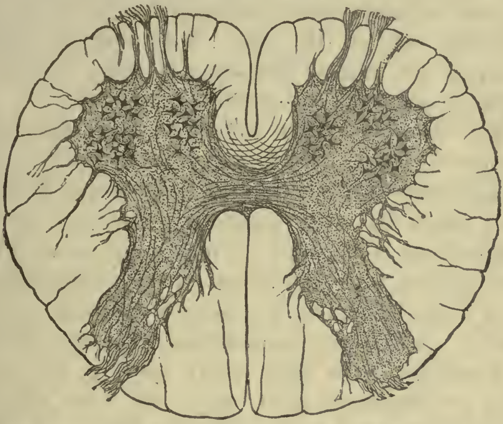


Transverse Sections of the Spinal Cord in Man.—I. Upper Cervical Region. II. Lower Cervical Region. III. Dorsal Region. IV. Lumbar Enlargement. V. Lower Extremity.

The nerve fibres of the gray substance are, in general, much smaller than those of the white substance, but otherwise present the same anatomical characters. Most of them run horizontally, in a transverse, antero-posterior, or radiating direction. They consist, first, of fibres which have penetrated the gray substance from the anterior and posterior nerve roots; secondly, of fibres which cross the median line in the gray commissure, both in front and behind the central canal, forming a commissural connection between the two lateral halves of the gray substance; and, thirdly, of fibres which run in a great variety of directions, and of which the origin and terminations are unknown.

The White Substance.—The white substance of the spinal cord consists of nerve fibres, the large majority of which run in a longitudinal direction, forming tracts or "columns," designated, according to their situation, as the *anterior*, *lateral*, and *posterior* columns of the cord. In microscopic transverse sections of the cord, treated by hardening and staining preparations, the longitudinal fibres present the appearance of minute cylinders cut across; while those which are horizontal or oblique are seen in profile for a longer or shorter distance in the section.

FIG. 103.



TRANSVERSE SECTION OF THE SPINAL CORD IN MAN; lumbar region.

The *anterior* column, included between the anterior median fissure and the anterior nerve roots, consists in great measure of fibres from the anterior horn of gray substance on the opposite side. The transverse band of white substance, at the bottom of the anterior median fissure, is known as the *white commissure;* but this name is not entirely appropriate, since the fibres in question do not connect corresponding parts on the two sides. Those joining the right anterior column come from the gray substance of the left anterior horn; and those which enter the left anterior column come from the gray substance of the right anterior horn. The so-called white commissure is therefore in reality a decussation, connecting the anterior columns on each side with the gray substance of the opposite side of the cord.

The *lateral* column, occupying the space between the anterior and posterior nerve roots, derives its fibres from two sources. First, from the whole external border of the anterior horn and a small part of the posterior horn. The mode of origin of these fibres in the gray substance is unknown; but they pass out from it horizontally and obliquely and then become parallel with the remaining longitudinal fibres of the lateral column. Secondly, from the anterior nerve roots; some of whose fibres, after traversing the gray substance of the anterior horn, pass out from it in a lateral direction like those just described, and join the lateral column. At each level, therefore, although the great mass of fibres in the lateral column are longitudinal, there are always some which are oblique, emerging from the gray substance, to become longitudinal at a higher point.

The *posterior column*, limited by the posterior median fissure internally and by the posterior nerve roots externally, also consists of fibres from two sources—namely, first, fibres coming from the inner border of the posterior horn, the origin of which cannot be more precisely determined; and secondly, fibres coming, through the gray commissure, from the opposite side of the cord. According to Huguenin,* the posterior columns are formed altogether of these two sets of fibres, and do not receive any from the posterior nerve roots.

Connection of the Nerve Roots with the Spinal Cord.—The *anterior* nerve roots enter the spinal cord in a number of distinct bundles, which pass horizontally backward between the longitudinal fibres of the white substance and reach the *gray substance of the anterior horn.* Here their fibres spread out in a variety of directions; some of them passing inward, some outward, and some almost directly backward. The exact termination of these fibres has not been determined, except for a part of their number. All observers are agreed that some of the root fibres are directly connected with large nerve cells in the anterior horn; and according to Huguenin, each one of the three groups of cells in this situation receives such communicating fibres. A second portion of the anterior root fibres, described by Kölliker,† and accepted by others, after running outward to the external border of the anterior horn, pass into the white substance, and, turning upward, become part of the longitudinal fibres of the lateral column. A third portion still is composed of fibres which run directly backward toward the posterior horn, but whose termination is unknown.

The fibres of the *posterior nerve roots* penetrate the cord in one or two principal bundles, and pass immediately to the *gray substance of the posterior horn.* Here some of them curve inward, assume a transverse direction, and cross the median line, in the gray commissure, to the opposite side of the cord. Others become lost in the gray substance of the posterior horn and the base of the anterior horn, without its being possible to ascertain their exact destination; since the connection of nerve fibres with nerve cells is not seen in the posterior horns. Finally, a third portion of these fibres, according to Kölliker, change their direction and become longitudinal, still remaining in the gray substance and continuing their course in this direction for an unknown distance.

The anterior and posterior nerve roots, accordingly, resemble each other in one respect, namely, that their immediate destination in the cord is the gray substance of the corresponding horns. But the fibres of the anterior root unite with nerve cells in the anterior horn, or join the longitudinal tract of the lateral column; while those of the posterior root show no direct connection with nerve cells, but partly cross to the

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* Anatomie des Centres Nerveux. Paris, 1879, p. 266.

† Eléments d'Histologie Humaine. Paris, 1868, p. 344.

opposite side in the gray commissure, and partly become longitudinal in the gray substance of the same side.

Connections of the Spinal Cord with the Brain.

The connections of the spinal cord with the brain take place by a continuation of the fibres of its longitudinal columns, through the medulla oblongata and tuber annulare. But this continuation is not entirely a simple one, since the fibres of the various columns shift their position at the level of the medulla oblongata, and also exhibit at one point or another more or less complete decussations.

Decussation of the Pyramids.—Throughout the greater portion of the cord, its columns are formed almost exclusively of longitudinal fibres, and each column, examined in successive sections, retains its special form and position. But in the upper cervical region a change begins to show itself by which the fibres from the inner and posterior parts of the lateral column are directed obliquely inward and forward, through the base of the anterior horn of gray matter and behind the anterior column of the same side. Above the level of the second cervical vertebra this change increases in extent, so that bundles of fibres from the lateral column pass obliquely forward and upward, across the median line, to the opposite border of the anterior median fissure; thus taking the place, immediately next this fissure, previously occupied by the anterior column. As the same thing happens on both sides, there appear, in the lower part of the medulla oblongata, at the bottom of the anterior median fissure, alternating bundles of fibres, successively crossing from left to right and from right to left. This is the *decussation of the anterior pyramids;* and after its completion these bodies appear as two longitudinal bundles, next the anterior median fissure, and running forward to the tuber annulare. The anterior pyramids accordingly are not continuations of the anterior columns of the cord, although placed above them in linear series. Their fibres are derived mainly from the lateral columns of the opposite side; and they form, in the lower part of the medulla oblongata, a decussation which is visible externally because it takes place by distinct bundles of considerable size, alternating with each other on the median line.

Fig. 104.

Transverse Section of Human Spinal Cord; at the lower extremity of the decussation of the pyramids.

This transfer of fibres from the lateral columns to the anterior pyramids, next the median fissure, accounts for the change in form of the cord while passing from the cervical region to the medulla oblongata. At the cervical enlargement in the lower part of the neck (Fig. 102, II.) the cord is very wide transversely, owing partly, no doubt, to the root fibres of the great nerves of the brachial plexus, which have joined the lateral columns after traversing the gray substance of the anterior horn. But at the upper extremity of the cord (Fig. 102, I.) its transverse diameter diminishes and its antero-posterior diameter increases; since some of its fibres have left the lateral column to reach an anterior position on the opposite side.

Beside the decussating fibres of the pyramids derived from the lateral columns of the cord there are others which come from the posterior columns and the posterior horns of gray substance. The change in direction of these fibres takes place at a little higher level than that just described. It forms the upper portion of the decussation of the pyramids. The fibres, after leaving the posterior columns and horns, run forward and inward, cross the median line obliquely, like the preceding, and then join the anterior pyramids, forming their deeper and more lateral portions. As the pyramids reach the tuber annulare, therefore, they are composed superficially and toward the median line of fibres from the opposite lateral columns of the cord; while their deep-seated and external fibres come from the opposite posterior columns and horns.

The further continuation of the anterior pyramids is through the tuber annulare into the crura cerebri, of which they form the lowermost or superficial portion. This part of the crus cerebri, which is that visible at the base of the brain, sends its fibres mainly forward, upward, and outward, into the substance of the corpus striatum. But according to Huguenin a portion of the fibres on its external border, representing those which have come from the posterior columns and horns, pass behind the cerebral ganglia to reach the convolutions of the occipital lobe.

Deep-seated Portion of the Crura Cerebri.—The deep-seated or uppermost portion of the crura cerebri, is formed of fibres from the anterior columns of the cord, and from the anterior part of the lateral columns. The *anterior columns* of the cord are contiguous to the median fissure until their place is taken, as above described, by the obliquely decussating bundles of the anterior pyramids. In the medulla oblongata, they thus come to be placed farther outward and backward, and in passing through the tuber annulare they occupy a deep-seated position in its interior. Thence they run forward in the upper or deep-seated portion of the crura cerebri, and pass to the optic thalami. The remaining fibres of the *lateral column*, which have not taken part in the formation of the pyramids, continue their course upward, pass through the medulla oblongata and tuber annulare, and, finally, joining the deep-seated portion of the crura cerebri, reach in this way the optic thalami.

Inferior Peduncles of the Cerebellum.—The inferior peduncles of the cerebellum, or the "restiform bodies," are continuations from the main part of the posterior columns of the cord. As these columns diverge from each other at the medulla oblongata, leaving between them the space of the fourth ventricle, they present the superficial appearance of passing directly, on each side, from the cord to the cerebellum. But while all admit that a portion of each restiform body is derived from the posterior column of the cord, observers differ as to which portion is so derived; and according to the views of Clarke and Meynert,* the greater part undergo decussation in the interior of the medulla oblongata, so that the restiform body of the right side is formed of fibres from the left posterior column, and *vice versâ.*

The connections of the spinal cord with the brain, so far as they are known with certainty, may be accordingly stated as follows:

1. The greater part of the lateral columns, and a portion of the posterior columns, after bilateral decussation, form the anterior pyramids, which are continued in the superficial portion of the crura cerebri to the corpora striata.

2. The remainder of the lateral columns, together with the anterior columns, pass by the deep-seated portion of the crura cerebri to the optic thalami.

3. The main portion of the posterior columns, perhaps after decussation in the medulla oblongata, appear in the restiform bodies, and thus reach the cerebellum.

Transmission of Motor and Sensitive Impulses in the Spinal Cord and Nerves.

The methods adopted for determining the functions of particular tracts of the nervous system are twofold; first, by applying an artificial stimulus to the nerve or nervous tract, and observing the effect produced; secondly, by observing what nervous function is abolished when the tract is divided or destroyed. In the peripheral nerves, which are simply organs of transmission, both these methods yield definite results. In the central parts, they are sometimes complicated by the mutual relations of the gray and white substances.

Motor and Sensitive Transmission in the Spinal Nerves and Nerve Roots.—If, in a living animal, a mechanical or galvanic stimulus be applied to the anterior root of a spinal nerve, the effect of this irritation is a convulsive movement of the part to which the nerve is distributed. The muscular action is instantaneous, involuntary, and momentary in duration; and it is repeated with mechanical precision each time the stimulus is applied. It is usually unaccompanied by any indication of sensibility, and it is evidently a direct result of the excitement of the anterior root. This root is therefore said to be "excitable," because its irritation excites a movement in the corresponding parts.

Furthermore, if the anterior root of a spinal nerve be divided, while

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* Huguenin. Anatomie des Centres Nerveux. Paris, 1879, p. 233.

the remaining nervous connections are left untouched, the result is an immediate and total paralysis of voluntary movement in the muscles to which that nerve is distributed. At the same time, the power of sensibility is undiminished, and the animal is still capable of feeling the contact of foreign bodies or a galvanic current applied to the skin. If the anterior roots of a series of spinal nerves be thus divided, as, for example, those of all the lumbar and sacral nerves on one side, the above effect will be produced for the entire corresponding region of the body, and the whole posterior limb on that side will lose the power of voluntary motion while retaining its sensibility. This is not due to any loss of physiological properties in either the nerve or the muscles, since irritation of the nerve or nerve root, outside the point of section, still produces muscular contraction as before. All these facts prove that the path by which impulses for voluntary motion pass, from the spinal cord to a muscle, is exclusively the anterior root of the spinal nerve.

On the other hand, if the posterior root be irritated, a sensation is produced, more or less acute, according to the amount and quality of the irritation. This sensation, when of a certain intensity, is accompanied by movements. But these movements are of a reflex character, and not necessarily confined to the part to which the nerve is distributed; and if the corresponding anterior root have been divided, this part will remain motionless, while muscular contractions continue to be produced elsewhere. Such movements, accordingly, are not produced directly by irritation of the posterior root, but are caused indirectly by the reaction of the nervous centres. The only immediate result of irritation of a posterior nerve root is a sensation, and this root is therefore said to be "sensitive."

Moreover, if the posterior root be divided, the consequence is a loss of sensation in the corresponding region of the body. This is due simply to the rupture of communication between the integument and the nervous centres; since irritation of that part of the divided nerve which is still attached to the spinal cord produces a sensation as before. The posterior root of the spinal nerve is, therefore, in this part of the nervous system, the exclusive channel of transmission for sensitive impressions.

But beyond the situation of the spinal ganglia, the two roots unite in a common trunk. Here, the fibres of the anterior and posterior roots become so intermingled that they can no longer be separately irritated by artificial means. They pass, still associated in this manner, into the branches and subdivisions of the nerve; and only separate from each other again at its terminal ramifications, where the sensitive fibres are distributed to the integument and the motor fibres to the muscles.

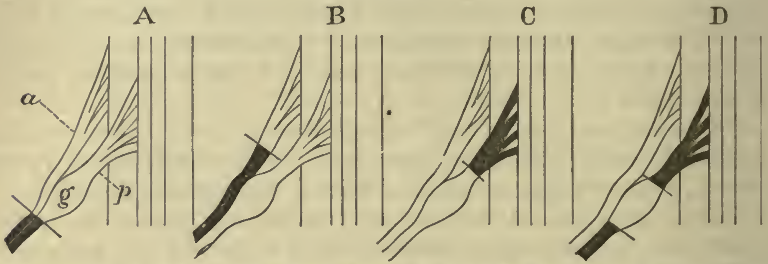
A spinal nerve, therefore, in its trunk and peripheral branches, contains both sensitive and motor fibres, and is consequently a "mixed" nerve. It is both excitable and sensitive, since its artificial irritation causes at the same time sensation and movement; and if it be divided, the injury is followed by loss of both sensibility and voluntary motion in the corresponding parts. It is also an important fact that, in these instances of section of the trunk, branches, or roots of a spinal nerve, the consequent loss of sensibility or motion is persistent, so long as the injury lasts. The nervous functions are not restored until the divided nerve fibres have gone through with the process of degeneration and regeneration, and have again acquired their natural continuity of texture. This shows that the suspension of functional activity is directly due to the injury of the nerve fibres, and not to the sympathetic action of other parts.

Centripetal and Centrifugal Degeneration of divided Nerve Fibres.—The degeneration of nerve fibres in a divided spinal nerve (page 353) takes place, below the point of section, throughout the peripheral portion of its trunk and branches, while its central portion, above the point of section, remains unaltered (Fig. 105, A). In this peripheral degeneration, all the fibres of the nerve, both sensitive and motor, are involved; and it is consequently plain that in both kinds their separation from the nervous centre has produced a disturbance of nutrition resulting in atrophy. Such a degeneration is "centrifugal;" that is, it affects the nerve fibres from the point of section outward. This expression does not imply a gradual extension of the process in that direction, since we know that in reality (page 354) it advances with the same rapidity throughout; but it indicates the fact that, after division of a spinal nerve, it degenerates between the point of section and the periphery, and not toward the nervous centre.

If the section be made, not upon the trunk of the nerve, but upon its *anterior* root above its junction with the posterior root, the same result takes place; that is, the divided fibres degenerate in a centrifugal direction, while that portion of the nerve root still connected with the spinal cord remains unaltered (Fig. 105, B). But in this case it is only the motor fibres in the nerve trunk which suffer degeneration; its sensitive fibres, derived from the posterior root, are not affected. After such a division, the degenerated motor fibres may be distinguished, in the nerve trunk and branches, from the unaltered sensitive fibres with which they are associated; and even after its inosculation with other nerves and subsequent ramification, the degenerated fibres belonging to the original nerve root may be recognized by their microscopic appearance. The degeneration or immunity of these fibres, therefore, depends on the severance or the preservation of their connection with the spinal cord.

But if the section be made on the *posterior* nerve root, between its ganglion and the spinal cord, the effect is reversed (Fig. 105, C). In this instance the portion of nerve root attached to the ganglion remains unaltered; that which is connected with the cord suffers degeneration, and the degenerated fibres can be traced to their entrance into the gray substance of the posterior horn. This degeneration is therefore "centripetal," since it takes place between the point of section and the spinal cord. The fibres of the posterior root degenerate wherever they are separated from connection with the ganglion; and if the ganglion be excised, they degenerate in both directions; namely, inward to the spinal cord and outward to the periphery (Fig. 105, D).

FIG. 105.



DEGENERATION OF SPINAL NERVES AND NERVE ROOTS AFTER SECTION.—A. Section of Nerve Trunk beyond the Ganglion. B. Section of Anterior Root. C. Section of Posterior Root. D. Excision of Ganglion. *a*. Anterior Root; *p*, Posterior Root; *g*, Ganglion.

These facts, first discovered by Waller,* have since been confirmed by all observers. They show that the nutrition of the anterior and posterior nerve roots is connected with different centres; since the fibres of the anterior root degenerate when separated from the gray substance of the anterior horn, while those of the posterior root degenerate when separated from the spinal ganglion. Such points are designated as "trophic centres," or centres of nutrition for the nerve fibres connected with them; indicating that the fibres preserve their normal structure so long as this connection is retained, and degenerate when it is cut off.

The nature of this relation between nerve fibres and their centres is unknown. We cannot assume that the nutrition of the fibres is immediately derived from the cells of the gray substance; since although the fibres of a divided nerve degenerate in the part separated from its centre, they are afterward regenerated by a process taking place, so far as we know, in the nerve itself (page 355). But it is a relation of great physiological importance, and extends to considerable tracts of white substance in the brain and spinal cord.

Motor and Sensitive Transmission in the Spinal Cord.—The simplest fact determined, in this respect, both by experimental research and pathological observation, is that the spinal cord is the exclusive organ of communication between the brain, on the one hand, and the external organs of sensation and motion, on the other; since if it be divided by a transverse section, compressed by fractured bone, or disorganized by disease at any part of its length, the result is a complete loss of sensibility and voluntary motion below the point of injury. The

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* Comptes Rendus de l'Académie des Sciences. Paris, 1851, tome xxxiii., p. 606; and 1852, tome xxxiv., p. 524.

general nervous function, performed by the cord as a whole, is therefore completely demonstrated, and is not subject to any doubtful interpretation.

But the precise path followed by motor and sensitive impulses in the spinal cord is much less easy of determination than in the nerve roots. The methods of investigation are the same in both instances; and are intended to ascertain, first; What parts of the spinal cord are sensitive or excitable under the application of artificial stimulus? and secondly; What parts are the natural channels of transmission for sensation and motion? The latter question is the more important in a purely physiological point of view; but the former is also of consequence as a guide in experimental research, and also for the explanation of pathological phenomena.

I. *What parts of the Spinal Cord are sensitive or excitable under the influence of artificial stimulus?*

The first portions of the cord which present themselves after opening the spinal canal are the *posterior columns.* The irritation of these columns by artificial stimulus, according to all observers, produces signs of sensibility. This sensibility is most marked in the immediate neighborhood of the posterior nerve roots; while at the greatest distance from this point, next the median line, it may be nearly absent. It is evident that the sensibility of the posterior columns is largely due to fibres of the posterior nerve roots, many of which traverse the outer portion of these columns in their passage toward the posterior horns of gray substance. The only discrepancy on this subject is in regard to the question whether the nerve roots are the only sources of sensibility for the posterior columns, or whether the longitudinal fibres of the columns have also a sensibility of their own. Irritation of the posterior columns, like that of sensitive tracts generally, sometimes produces movements in various parts; but these movements are reflex in character, and are the signs of an irritation communicated to the nervous centres.

Sensibility also exists, according to Vulpian, in that portion of the *lateral columns* contiguous to the posterior nerve roots. But as the irritation is applied to points farther forward, the signs of sensibility rapidly diminish, and soon disappear altogether. In all these parts, of both posterior and lateral columns, the sensibility is most marked, or even exclusively situated, in their superficial portions; and experimenters are generally agreed that the *gray substance* of the cord, throughout, is destitute of sensibility under the application of artificial stimulus.

Whatever minor points, therefore, may remain in doubt, the principal fact is unquestioned, namely, that the posterior parts of the spinal cord, consisting of the posterior columns and the adjacent half of the lateral columns, are sensitive to irritation, especially at their surface; and accordingly inflammation of the meninges, or other diseased action in this locality, may be accompanied by painful irritation of the spinal cord. The irritation thus produced is still more liable to cause pain, on account of the attachment at the surface of the cord of the posterior nerve roots, which are themselves acutely sensitive.

The properties shown by the *anterior columns* on the application of artificial stimulus are, on the whole, quite different from those of the posterior columns. There is some difference in the results obtained in this respect by experimenters. This difference mainly consists in the fact that, according to the large majority (Magendie, Longet, Bernard, Brown-Séquard, Vulpian, Flint), irritation of the anterior columns produces convulsive movement in the parts below; while others (Calmeil and Chauveau) have found these columns inexcitable. But in such instances experiments with a positive result are more decisive than those which are negative, since the excitability of the anterior columns might be suspended by opening the spinal cord, or by other incidental conditions; but nothing of this kind could confer upon them a property which they did not naturally possess.

There can be no doubt, accordingly, of the excitability of the anterior columns. This excitability, while producing convulsive movements in the parts below, is in most instances unaccompanied by sensibility. The absence of pain, in cases where the convulsive action is well marked, has been especially noticed by Flint,* and is mentioned by various other writers.

The sensibility of these parts, sometimes observed, is slight in degree, and is frequently suspended or abolished by exposure of the spinal cord.

The *lateral columns* are also excitable in their anterior portions, near the anterior nerve roots; while toward their posterior portions, according to Vulpian, the excitability diminishes, and gradually gives place to the phenomena of sensibility characteristic of the posterior parts of the cord.

The anterior and posterior portions of the cord are therefore distinguished, in great measure, by their mode of reaction toward external irritation. The anterior and lateral columns, on each side of the anterior nerve roots, are excitable, and produce movement on being irritated; and both the posterior and lateral columns, near the entrance of the posterior nerve roots, are endowed with sensibility. Inflammatory or other irritation of the meninges, over any part of the anterior aspect of the cord, may accordingly cause convulsive movement in the limbs below; and either pain alone or convulsions alone may be the symptoms of inflammatory irritation of the posterior or anterior portions of the cord respectively. But the morbid action most frequently extends to both regions, and disturbances of sensibility and motion are present at the same time, or at different periods in the disease.

II. *What parts of the Spinal Cord are the natural channels for sensation and movement?*

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* Physiology of Man; Nervous System. New York, 1872, p. 276.

This question cannot be settled by applying an artificial stimulus to various parts of the cord. Such experiments can only determine the sensibility or excitability of a nervous tract, but not its function as a channel of transmission. A nervous tract might be sensitive to external irritation, and yet the natural impulses of sensation, coming from the periphery, might follow a different route. On the other hand, a part might be capable of transmitting impulses of sensation or motion, received from corresponding nerve fibres, and yet might not itself be either excitable or sensitive. In the peripheral nerves and nerve roots, the two sets of properties coexist. The posterior roots, which transmit sensation, are themselves sensitive; and the anterior roots, which transmit the stimulus of motion, are excitable. But although these properties are connected in the nerves and nerve roots, they are not necessarily so in the nervous centres; and investigation shows that in the spinal cord they are often independent of each other.

The only experimental method of ascertaining the natural path, in the spinal cord, for sensitive and motor impulses respectively, is to divide or destroy different portions of the cord, and to observe which of these injuries is followed by the loss or preservation of sensation or movement. Even these experiments are not always decisive; since different parts of the white and gray substance are liable to influence each other by sympathetic action. If division of one column of the spinal cord be followed by loss of sensibility, we cannot at once assume that the column in question is the organ of its transmission; because the loss of sensibility may be temporary, and due to the shock inflicted upon neighboring parts. The most decisive experiments, accordingly, for determining the channels of sensation and motion in the spinal cord, are those in which these functions have remained, notwithstanding the destruction of certain parts of the cord.

By investigating in this way the channels for *sensation* in the spinal cord, the first fact, demonstrated in such a manner as to be generally accepted, is that after division of the posterior columns the power of sensibility is undiminished, and the animal continues to feel impressions made upon the integument of the corresponding parts. This result, which was obtained by several of the older experimenters, is fully confirmed by the observations of Brown-Séquard* and Vulpian.† The posterior columns therefore are not the channels for ordinary sensitive impressions, notwithstanding their own sensibility to artificial irritation. The converse of this experiment, namely, transverse division of all parts of the cord excepting the posterior columns, as performed by the same observers, is followed by complete loss of the power of sensation.

On the other hand, if both the anterior and lateral columns of white

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* Physiology and Pathology of the Central Nervous System. Philadelphia, 1860, p. 19.

† Système Nerveux. Paris, 1866, p. 373.

substance be divided, leaving only the posterior columns and the gray substance, sensibility remains; and Brown-Séquard has varied the mode of procedure by dividing both anterior, lateral, and posterior columns in the same animal at different levels, so that the continuity of the cord as a whole is preserved by the gray substance, while all the longitudinal tracts of white substance are divided. In this case sensibility remains, although diminished in intensity.

The transmission of sensitive impressions, therefore, takes place through the gray substance. This substance, which is itself insensible to direct irritation, forms the medium of communication between the peripheral sensitive nerves and the brain above. It is not known whether this communication be made by longitudinal fibres running continuously through the gray substance, or by successive connections of the nerve cells.

The channels for *voluntary motion* in the spinal cord are mainly in the posterior part of the lateral columns. These tracts have been shown (page 385) to be continuous at the medulla oblongata with the anterior pyramids and their prolongations above. They are therefore known as the "pyramidal tracts;" and they form the medium of communication between the brain and the origin of the motor nerves in the gray substance of the spinal cord. This has been established by a variety of investigations, carried on by different methods. It is certain, in the first place, that the *posterior* columns take no direct part in the act of voluntary motion, since after their complete section this power remains unimpaired; and according to Brown-Séquard, if all the rest of the cord be divided, leaving the posterior columns untouched, voluntary motion is lost in the parts below. There remain therefore only the lateral and anterior columns of white substance which can serve as tracts of communication for voluntary impulses.

This question has received further elucidation from the study of *secondary degenerations* in the spinal cord, first observed by Türck* in 1851. These degenerations are similar to those of the spinal nerves and nerve roots, when separated from their trophic centres. They take place, both in the brain and spinal cord, in consequence of the destruction, by a primary disorder, of certain nerve centres or the intervening parts; and they are therefore known as "secondary" degenerations. They extend for long distances through the cerebro-spinal axis, involving the tracts connected with the part primarily diseased; and these degenerated tracts can then be distinguished from the healthy white substance by which they are surrounded.

As in the nerves and nerve roots, secondary degenerations in the spinal cord, may be ascending or descending. *Ascending* degenerations are those which extend from the primary lesion upward to the brain and are therefore centripetal. *Descending* degenerations extend from the point of lesion downward through the cord, and are therefore centrifugal.

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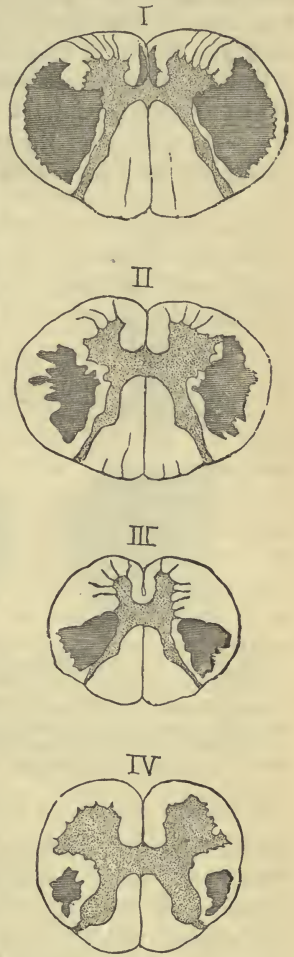
* Sitzungsberichte der Akademie der Wissenchaften. Wien, 1851, Band vi., p. 288.

Destructive lesions in certain parts of the brain are followed by descending secondary degenerations, through the crura cerebri, the anterior pyramids, and the posterior parts of the lateral columns of the cord, that is through the entire length of the pyramidal tracts. Such a condition causes paralysis of voluntary movement, without diminishing the power of sensibility. If the degeneration be confined to one lateral half of the spinal cord, paralysis exists only on that side; if it be bilateral both sides of the body are paralyzed. Similar descending degenerations may take place from any point where a lesion exists in the pyramidal tracts, and according to Charcot * these tracts may also be affected by a primary alteration throughout their extent in the medulla oblongata and spinal cord.

FIG. 106.



TRANSVERSE SECTIONS OF THE SPINAL CORD; showing degeneration of the Pyramidal Tracts; from a patient with bilateral paralysis. (Charcot.) I. Upper part of Cervical Enlargement. II. Lower Cervical Region. III. Dorsal Region. IV. Lumbar Enlargement. The degenerated portions are shaded in transverse lines. In Section I., the Columns of Türck are visible at the inner edge of the anterior columns.

As the pyramidal tracts, in descending through the medulla oblongata, reach the decussation of the pyramids, a portion of their fibres is continued upon the same side of the median line, forming a narrow band on the inner border of the anterior column. These bands are the *Columns of Türck* (Fig. 106, Section I.). They rapidly diminish in size from above downward, and in man come to a termination in the lower part of the cervical region. The greater part of the pyramidal tract crosses the median line at the decussation of the pyramids to the opposite side, and is thence traceable quite to the lower extremity of the cord. In the cervical region it occupies most of the lateral columns, but in the dorsal region is confined to its posterior half, and in the lumbar region is still further reduced. Its fibres no doubt leave it at successive points from above downward, to enter the gray substance of the anterior horn.

The preceding facts are derived from pathological anatomy. But similar results

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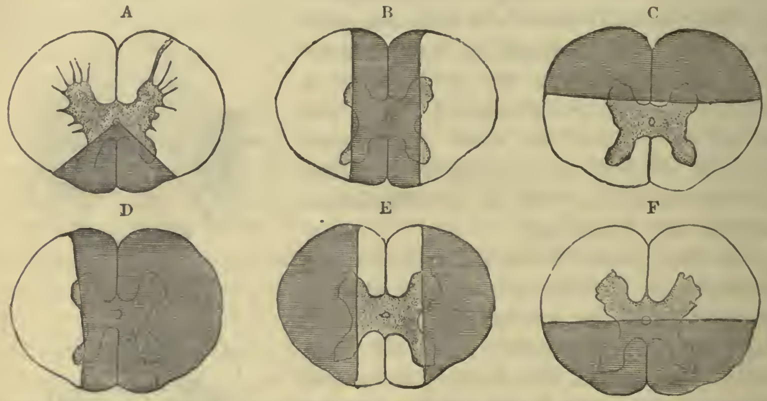
* Leçons sur les Maladies du Système Nerveux. Paris, 1877, tome ii., p. 219.

have been obtained by Schiefferdecker* in dogs after section of the spinal cord in the dorsal region, with consequent paralysis of the posterior limbs. The degeneration of the pyramidal tracts in these cases was constant, and always in a descending direction, from the point of section to the lower extremity of the cord.

Finally, in the experiments of Woroschiloff† on the rabbit, the function of the pyramidal tracts in the lateral columns was investigated by partial sections of the spinal cord in the dorsal region. The main results of these experiments are as follows:

FIG. 107.



PARTIAL SECTIONS OF SPINAL CORD OF RABBIT, IN LOWER DORSAL REGION.—A, B, C. Without Paralysis. D, E, F. With Paralysis. A. Section of Posterior Columns. B. Section of Anterior and Posterior Columns and Gray Substance. C. Section of Anterior half of Cord. After all these sections the animal uses his hind legs freely in locomotion. D. Section of the entire cord except left lateral column; paralysis of right hind leg, preservation of motion in left. E. Section of both lateral columns; paralysis of both hind legs. F. Section of posterior half of cord; paralysis of both hind legs. (Woroschiloff.)

Voluntary motion in the posterior limbs remains unimpaired after 1st, Section of both posterior columns (Fig. 107, A); 2d, Section of both anterior and posterior columns and the gray substance (B); and 3d, Section of the anterior half of the cord on both sides (C). That is, every part of the cord, excepting the posterior half of the lateral columns, may be divided in the dorsal region without causing paralysis of the hind limbs. On the other hand this paralysis is produced by section of both lateral halves of the cord outside the gray substance (E), and by section of the posterior half of the cord on both sides (F); and lastly, division of the whole cord excepting one lateral column (D), leaves the hind limb on that side capable of movement while the opposite limb is paralyzed. The transmission of voluntary impulses in the spinal cord takes place therefore through the pyramidal tracts,

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* Archiv für pathologische Anatomie und Physiologie. Berlin, 1876. Band lxvii., p. 542.

† Arbeiten aus der physiologischen Anstalt zu Leipzig. Jahrgang, 1874. Leipzig, 1875, p. 99.

occupying above the dorsal region the larger part of the lateral columns, and in the remainder of the cord their posterior half.

Similar experiments have been performed by Ott* on the spinal cord of the rabbit in the cervical region, with results essentially like those above detailed, excepting that the effects of paralysis were exhibited in the anterior limbs as well as the posterior, and that there was evidence of a certain amount of decussation of the motor tracts in the cervical portion of the cord.

Descending degenerations of the pyramidal tract, according to Charcot, do not usually extend to the motor nerves or nerve roots. From this it is inferred that the pyramidal fibres terminate in the gray substance of the anterior horns, while the nerve roots consist of new fibres originating from the gray substance. The nerve root therefore degenerates only when divided beyond the point of its emergence from the anterior horn.

Crossed Action of the Spinal Cord.

The spinal cord, as a medium of communication between the brain and the peripheral organs, exerts a crossed action. Sensitive impressions received by the integument on one side of the body are conducted through the cord to the opposite side of the brain; and motor impulses originating on one side of the brain pass to the nerves and muscles on the opposite side of the body. This is established both by experiment on animals and by pathological observation in man; since lesions on the right side of the brain cause paralysis, both of sensation and motion, on the left side of the body, and *vice versâ*. These two functions may be paralyzed either together or separately, according to the locality and extent of the injury to the brain; but when the paralysis is distinctly confined to one side of the body, the alteration of nervous tissue upon which it depends is found after death on the opposite side of the brain.

Decussation of the Motor Tracts.—It may be said, in general terms, that the transmission of voluntary motor impulses, in the spinal cord, takes place continuously upon the same side. That is, if a transverse section of one lateral half of the cord be made at any point in the lumbar, dorsal, or cervical region, a paralysis of voluntary motion is produced on the same side for all parts below the level of the injury. This observation, first made by Galen,† has been confirmed by all subsequent experimenters. Each side of the body therefore derives its power of voluntary motion from the pyramidal tract in the corresponding half of the spinal cord. But at the decussation of the pyramids, in the medulla oblongata, these tracts cross to the opposite side, afterward continuing their course, through the tuber annulare and crura cerebri, to the brain. A lesion of the motor tract accordingly

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* American Journal of the Medical Sciences. Philadelphia, October, 1879.

† De Locis Affectis. Liber III., Cap. xiv.

varies in effect according to its situation. If seated in the spinal cord, it produces paralysis on the same side of the body; if above the decussation of the pyramids, in the medulla, tuber annulare, crus cerebri, or cerebral hemisphere, it produces paralysis on the opposite side; and, finally, a lesion involving the decussation of the pyramids causes paralysis on both sides of the body at once.

These are the general results of both experiment and observation, and they express the most habitual and important conditions of unilateral and bilateral paralysis. But there are certain variations from the type of simple and complete decussation which have some influence on the phenomena.

First, the study of descending degenerations of the pyramidal tract shows that, beside the principal mass of fibres in this tract which cross to the opposite side of the cord at the decussation of the pyramids, there are a certain number which continue downward on the same side, forming in the cervical region the "columns of Türck" (Fig. 106). These direct fibres are in small proportion, representing, on the average, considerably less than ten per cent. of the whole pyramidal tract, and in man they do not extend, as a rule, below the cervical region. What becomes of them here is unknown; but it is evident that their destination may be twofold. They may terminate in the anterior horns of gray substance; in which case the decussation of the pyramidal tracts would be partial, and the upper limb would receive some motor power from the same side of the brain. Or they may finally cross, through the white commissure, to the opposite side of the cord; in which case the decussation would be complete, a part of it taking place below the pyramids, in the cervical region. This would explain the results obtained by various experimenters (Van Kempen, Brown-Séquard, Vulpian), who have found that in animals a division of one lateral half of the spinal cord in its upper portion is followed by a certain degree of paralysis on the opposite side. All, however, are agreed, that this effect is not produced by a similar section in the lumbar region, but slightly or not at all in the dorsal portion, and is only pronounced after a section in the cervical region.

Secondly, The proportion between the direct and crossed fibres of the pyramidal tract, in man, may vary in exceptional cases, so that the majority of these fibres may be direct, and only the minority decussate. Under these conditions, a lesion in the brain, contrary to the general rule, would cause paralysis on the same side of the body. According to Charcot* such instances exist, although their occurrence is extremely infrequent. Similar exceptional variations have been recorded in regard to other decussating tracts in the nervous system.

Decussation of the Sensitive Tracts.—Sensitive impressions, passing from the integument to the nervous centres, undergo, like the motor

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* Leçons sur les Localisations dans les Maladies du Cerveau et de la Moelle épinière. Deuxième Partie. Paris, 1880, p. 195.

impulses, a bilateral decussation; since lesions of the brain above the medulla oblongata cause diminution or loss of sensibility on the opposite side of the body.

But while the tracts for voluntary motion have a continuous unilateral course in the spinal cord, and decussate only or principally at the medulla oblongata, those for sensation cross the median line at successive points throughout the length of the cord. This is shown by the fact that a transverse section of one lateral half of the cord, which paralyzes motion on the same side, causes loss of sensibility on the opposite side; while the power of sensation remains on the side of the injury. If a section of one lateral half of the spinal cord be made at the lower end of the dorsal region on the right side, the right hind leg is paralyzed of motion but retains its sensibility; the left hind leg, at the same time, retains its power of motion but loses its sensibility. Furthermore, sensibility is not only retained on the side of the section in these cases, but is perceptibly exaggerated; so that an impression upon the skin is perceived on that side more acutely than before the section.

These results, which were partially obtained by several of the older experimenters, were first distinctly brought out by Brown-Séquard. According to his experiments, the phenomena are so complete as to imply an entire crossing of the sensitive tracts in the spinal cord. Other observers have found the appearances less decisive; Vulpian, among others, maintaining that loss of sensibility on the opposite side, after section of a lateral half of the cord, is only partial, and that sensitive impressions conveyed through the gray matter may continue to pass even after one lateral half of the cord has been divided in the dorsal, and the other in the cervical region, by two sections at a considerable distance from each other.

It is certain, however, that after section of one lateral half of the cord the phenomena which indicate a crossing of the sensitive tracts are distinctly marked. We have found that after such a section, in the dog, in the dorso-lumbar region, the difference in sensation and motion between the two sides is very striking. Sensibility is either lost or very much diminished on the opposite side, while on the side of the section, there is complete muscular paralysis and increased sensibility.

What causes the increase of sensibility, after section of one lateral half of the spinal cord? It is probably due to local irritation of the gray substance at the point of section, producing in this way an apparent exaggeration of sensitive impressions on that side. For this purpose it is not necessary to make a complete section of the lateral parts of the cord; since Brown-Séquard has found that division of the posterior columns alone will cause increase of sensibility, more or less pronounced in different cases; and according to Vulpian, the same effect may be produced by simply pricking with a pointed instrument the posterior or lateral parts of the cord on one side.

The crossing of the sensitive tracts, according to Brown-Séquard, is especially demonstrated by the effects of a longitudinal section in the median line. Such a section in the lumbar region of the cord, separating at that point its two lateral halves from each other, is followed by complete loss of sensibility in both hind legs. This result alone would not be decisive, since the suspension of sensibility might be due to the shock of the operation; but it is of much value in connection with the fact that, although sensibility is lost, the power of voluntary motion is retained in both posterior limbs.

Finally, instances in man, where a lesion of the spinal cord is accompanied by loss of voluntary motion on the same side and loss of sensibility on the opposite side, confirm the results derived from experiment on animals. The decussation of both motor and sensitive tracts is complete in the upper part of the medulla oblongata; but below this point the cord acts as a conductor for motor impulses going to the muscles on the same side, and for sensitive impressions coming from the integument of the opposite side.

Various forms of Paralysis, from lesions of the Cerebro-spinal Axis.—In consequence of disease or injury in the cerebro-spinal axis, a variety of symptoms may be produced affecting sensation and motion. The principal forms of paralysis from this cause are, first, "paraplegia," or paralysis of the lower portion of the body and lower limbs; and secondly, "hemiplegia," or paralysis of one lateral half of the body, and of one or both limbs on the corresponding side.

I. In *Paraplegia*, the injury affects the whole substance of the spinal cord at a particular level, and the result is loss of sensation and voluntary motion on both sides, for all parts below the level of the injury. If the lesion occupy the lumbar portion of the cord, the legs and the pelvic regions are paralyzed and insensible, while the arms and the rest of the trunk are unaffected. If it be in the dorsal region, a corresponding part of the abdomen and thorax is also deprived of sense and movement; and if situated in the middle cervical region, it produces paralysis and insensibility of both upper and lower limbs, as well as of the chest and intercostal muscles. A paralysis of this kind, involving the arms and the intercostal muscles, is more dangerous than that of the legs alone; because a slight extension of the lesion will reach the origin of the phrenic nerves, and produce death by stoppage of respiration.

In complete paraplegia, sensation and motion are both abolished in the affected parts; and injury or disease in the spinal cord, when sufficient to destroy one of these functions, almost necessarily reaches the parts which preside over the other. But in slight or incomplete cases, either sensibility or movement may be more or less affected, according to the intensity of the lesion in different parts of the cord.

II. In *Hemiplegia* of the simplest form, there is loss of sensation and voluntary motion in one upper and lower limb, and in the integument and muscles of the trunk on the corresponding side. It is, therefore, a complete paralysis of one lateral half of the body; the affection being limited by the median line, both in front and rear. In such cases the lesion is on the opposite side, above the decussation of the anterior pyramids; namely, in the upper part of the medulla oblongata, the crura cerebri, the cerebral ganglia, or the hemispheres. It is most frequently seated in the cerebral ganglia or the hemispheres.

In hemiplegia from this cause, the loss of sensibility and the loss of motion occupy the same half of the body, though they are not always equally well marked. When the lesion, on the other hand, is in one lateral half of the spinal cord, there is loss of motion on the corresponding side of the body, and loss of sensibility on the opposite side. A number of such cases have been collected by Brown-Séquard, in which the situation of the injury was ascertained by post-mortem examination.

Furthermore, a distinction is made between affections involving loss of motion and those accompanied by loss of sensation. The term *paralysis* indicates more especially an impairment or abolition of the power of voluntary movement; while diminution or loss of sensibility is called *anæsthesia.* Either of these affections may be complete or partial; confined to particular regions, or extending over a considerable part of the body. They may be present together, as in paraplegia; or either may exist independently, as local paralysis or local anæsthesia. A loss of sensibility occupying one lateral half of the body is known as *hemianæsthesia;* and as shown above, it may be associated with hemiplegia in the same region, or the two may coexist on opposite sides.

The Spinal Cord as a Nervous Centre.

So far as the spinal cord is concerned in sensation and voluntary motion, it acts as a medium of communication between the brain and the external parts. Its complete division at any point destroys this communication; so that the commands of the will are no longer transmitted to the muscles, and impressions made upon the integument produce no conscious sensation. But after such an operation motion is not altogether abolished in the limbs; and sensitive impressions, though no longer perceived by the individual, are still capable of exciting muscular reaction. These phenomena, which take place without the intervention of the brain, result from the action of the cord as a nervous centre, and are due to the independent properties of its gray substance.

Reflex Action of the Spinal Cord.—If a decapitated frog be allowed to remain at rest for a few moments, until the effects of nervous shock have passed off, movement can be excited in the limbs by applications made to the integument. If the skin of one of the feet be pinched with forceps, or immersed in a weak acidulated solution, the leg is immediately drawn up toward the body, as if to escape the source of irritation. If the stimulus be of slight intensity, the corresponding leg only will move; but if it be more severe, motion will often be produced in the opposite limb, or even in all the limbs at once. These phenomena may be repeated a great number of times, until the irritability of the nervous system is exhausted, or until some structural change has taken place in the tissues.

In the movements thus produced after decapitation there are two important peculiarities:

First, they are never spontaneous; but are excited only by the application of an external stimulus. The decapitated frog, if left to itself, remains motionless, in a nearly natural attitude, without any tendency to alter its position. Each application of stimulus causes a movement, after which the limbs resume their condition of quiescence, until a repetition of the stimulus calls out a new movement.

Secondly, the action is not produced by direct excitement of the muscles. The stimulus is applied to the integument of the foot, and the muscles of the leg and thigh contract in consequence. This shows that both sensitive and motor nerves take part in the process. The sensitive fibres of the integument receive the impression and convey it inward; after which the motor fibres transmit an outward stimulus to muscles in a different part. Even other limbs, as already mentioned, may be set in motion by an irritation applied to the integument of one.

Furthermore, the nervous action is not transmitted, in these cases, directly from the integument to the muscles; it passes through the spinal cord, which thus forms a link in the chain of communication. For if the posterior limb be left uninjured, while its connection with the cord is severed by dividing the sciatic nerve in the abdomen, no further action can be excited, and the limb remains motionless whatever irritation be applied to the integument.

Lastly, if the spinal cord be destroyed by a stilet introduced into the spinal canal, this also puts an end to the phenomena, and irritation of the integument will no longer produce muscular reaction in the limb. The muscles can then be excited only by a stimulus applied to themselves, or to their motor nerves.

These facts show that the phenomena in question are due to a reflex action, in which three different nervous elements take part; namely, first, the sensitive nerve fibres, conveying an impression inward from the integument; secondly, motor nerve fibres, transmitting a stimulus outward to the muscles; and, thirdly, a nervous centre between the two, in which the reflex action is accomplished. The nervous centre, in this instance, is the gray substance of the spinal cord.

It is evident, accordingly, that consciousness is not necessary for the reception of sensitive impressions by a nervous centre; and also that motor impulses may originate in a nervous centre without volition. The reflex action of the spinal cord is both unconscious and involuntary; and yet it is completely efficient, and produces muscular action at once on the application of a stimulus to the skin.

Diminution or Increase of Reflex Action in the Cord.—The reflex action of the spinal cord, like other forms of nervous activity, may suffer temporary depression or suspension by shock or injury to the system at large. Decapitation in the frog is often followed, for a few moments, by an interval of nervous paralysis, in which no phenomena of reaction can be obtained. Even injuries in which the nervous centres are not directly interested, such as opening the abdomen and removing the abdominal organs, may produce a similar effect. In some instances this period of depression is very short, so as to be almost imperceptible; in others it lasts for several minutes. After it has passed off, the reflex irritability of the cord returns, and, if the cord itself have been wounded or divided, may even be perceptibly increased in intensity.

It is for this reason that reflex action often seems more vigorous and prompt in the frog after removal of the head, or after transverse division of the cord at its upper part. The wound induces an increased excitability, in consequence of which sensitive impressions produce a more energetic reaction. This is shown by the observations of Türck, Bernard, and Vulpian, in which, after section of one lateral half of the cord, the hind leg on that side is withdrawn more rapidly from an acidulated solution than the other; and in which reflex action, in decapitated animals, becomes more marked, in consequence of successive transverse sections, in the cervical and dorsal regions.

The reflex action of the cord may be increased by poisonous substances. Strychnine is the most efficient in this respect, and produces an exalted irritability of the spinal cord, in consequence of which a slight irritation of the skin is followed by excessive muscular reaction. In a decapitated frog, under ordinary conditions, the reflex action of the cord is distinct but moderate in degree. Slight irritations have but little effect, and the pinching of one hind foot usually causes retraction of that limb only. But if a solution of strychnine be injected beneath the skin, at the end of ten or fifteen minutes, when absorption has taken place, the reflex irritability of the cord is exaggerated in a marked degree. The animal still remains motionless if undisturbed; but the least irritation applied to the skin, such as the contact of a hair or a feather, or the jar produced by a blow upon the table near by, will often cause violent convulsions, in which all the limbs take part. As these effects are produced in the decapitated animal, they are independent of the action of the brain. Strychnine, accordingly, acts upon the spinal cord by increasing its excitability, thus causing convulsive movement from slight external irritation.

Similar results may follow, as a secondary consequence, from wounds or injuries either of the spinal cord or of peripheral nerves. Brown-Séquard* has shown that in guinea-pigs a section of one lateral half of the cord sometimes produces, after a few weeks, such a condition of the nervous centres that epileptiform convulsions, of very intense character, may be excited by pinching the skin of the face and neck, on the corresponding side. The phenomena of tetanus in man, following

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* Researches on Epilepsy. Boston, 1857.

wounds of peripheral nerves, are also reflex. The tetanic spasm is usually, if not always, excited by an external cause; and this cause may be so slight that in the healthy condition it would have no perceptible effect. The accidental movement of the bedclothes, the shutting of a door, the passing of a carriage in the street, or even a current of air upon the skin, may be sufficient to throw the muscular system into spasmodic action. The irritability of the spinal cord as a nervous centre is, therefore, liable to be increased or diminished by causes acting upon it from without.

Reflex Action of the Cord in Warm-blooded Animals and in Man.—In the frog and other cold-blooded animals, the reflex action of the spinal cord lasts for a considerable time after death; often continuing, if the animal be kept in repose and sufficiently cool and moist, for twenty-four hours or longer. In the warm-blooded animals, it disappears more rapidly; and it must be sought for, if at all, within a short time after death, since a nearly constant supply of blood is essential in these animals to the irritability of the nervous system. But if the circulation be maintained by means of artificial respiration, the reflex action of the cord will continue, independently of the brain; and although sensation and volition are absent, movements of the leg may be produced by pinching the skin of the foot.

Robin* has observed the reflex action of the spinal cord, after decapitation, in man, in the case of an executed criminal whose body was subjected to examination. The muscular contractions were produced about one hour after execution. "While the right arm was lying extended by the side, with the hand about 25 centimetres distant from the upper part of the thigh, I scratched with the point of a scalpel the skin of the chest at the areola of the nipple, for a space of 10 or 11 centimetres in extent, without making any pressure on the subjacent muscles. We immediately saw a rapid and successive contraction of the great pectoral muscle, the biceps, probably the brachialis anticus, and lastly the muscles covering the internal condyle.

"The result was a movement by which the whole arm was made to approach the trunk, with rotation inward and half-flexion of the forearm upon the arm; a true defensive movement, which brought the hand toward the chest as far as the pit of the stomach. Neither the thumb, which was partially bent toward the palm of the hand, nor the fingers, which were half bent over the thumb, presented any movements.

"The arm being replaced in its former position, we saw it again execute a similar movement on scratching the skin, in the same manner as before, a little below the clavicle. This experiment succeeded four times, but each time the movement was less extensive; and at last scratching the skin over the chest produced only contractions in the great pectoral muscle which hardly stirred the limb."

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* Journal de l'Anatomie et de la Physiologie. Paris, 1869, p. 90.

The neck had been severed, in the above case, near the level of the fourth cervical vertebra.

Reflex action may also be seen, in man, in certain cases of disease of the spinal cord. If the upper portion of the cord be disintegrated by inflammatory softening, so that its middle and lower portions lose their connection with the brain, paralysis and insensibility ensue in all parts below the seat of the lesion. Under these conditions, the patient is incapable of voluntary motion in the paralyzed parts, and is unconscious of any injury to the integument in the same region. But if the soles of the feet be gently irritated with a feather or with the point of a needle, a convulsive twitching of the toes will often take place, or even retractile movements of the leg and thigh; and such movements may frequently be excited by the sudden contact of cool air with the lower limbs. We have repeatedly witnessed these phenomena, in disease of the spinal cord, where the paralysis and insensibility of the lower limbs were complete. Many similar instances have been reported by various authors.

Physiological Action of the Spinal Cord as a Nervous Centre.—The reflex action of the spinal cord, as it takes place in the healthy condition, is not easily brought under observation. In animals, unless the head be removed or the spinal cord separated from the brain, reflex and voluntary movements are liable to be confounded; and in man during health, the phenomena of sensation and volition are so prominent as to obscure those which are independent of the will. Nevertheless, the latter are exceedingly important, and many of them in almost constant operation.

The general character of reflex actions of the spinal cord is that they tend unconsciously to the *defence or preservation* of the body. This is seen in the simplest experiments on animals. If a decapitated frog be suspended in the air, the posterior limbs hang downward in a perfectly relaxed condition. On pinching one of the feet, or immersing it in acidulated water, the limb is retracted by its flexor muscles, the result being a withdrawal of the foot. The muscles then relax, and the limb lengthens until the foot touches the irritating liquid, when it is again drawn up; and so on, until the irritability of the cord is so far diminished that it no longer reacts. In this case, therefore, the only muscles thrown into activity are the flexors, which tend to withdraw the foot from the source of irritation. When an irritation is applied to the side of the trunk, it is common to see a hind foot brought to the irritated spot, as if to protect it; and in some instances the adaptation of reflex movements to accomplish a definite result is very marked. This cannot be attributed to any faculty of perception in the spinal cord; since we know, from pathological cases in man, that when the cord is separated from the brain by disease or injury, the parts below are absolutely deprived of sensibility and volition. The movement produced therefore depends simply on the structure of the limbs and the nervous mechanism of the spinal cord. In the case of reflex action observed by Robin in a decapitated criminal, the effect of irritating the skin over the chest was a flexion and inward rotation of the arm and forearm; and this necessarily brought the hand near the point irritated. It is evident that the connection of sensitive fibres with motor fibres, through the gray substance of the cord, may be such as to call into action particular muscles, without the intervention of consciousness or voluntary impulse. This is the character of the reflex action of the spinal cord.

As a general rule, movements of flexion are adapted to protect the part from external injury, and are excited by moderate causes; those of extension are calculated to repel the foreign substance or to escape from it by moving the whole body, and are called out by unusual or excessive stimulus. The defensive character of these movements is frequently manifest, in a state of health, when the brain takes no part in their production. If the surface of the skin be unexpectedly brought in contact with a heated body, the injured part is often withdrawn by a rapid and convulsive movement, before we feel the pain, or fairly understand the cause of the involuntary act. Whenever the body accidentally loses its balance, the limbs are thrown into a flexed position, calculated to protect the exposed parts and to break the fall, by a similar involuntary movement. Notwithstanding, therefore, the evident utility of these actions, they have no intentional character, and are performed without distinct consciousness of their object.

The spinal cord has also an important action in regard to *attitude* and *locomotion*. The preservation of the attitude alone requires the harmonious action of many different muscles, all of which contribute to the position of the body. This is especially the case in man, where, in the standing posture, the body is balanced upon its narrow supports, preserving its equilibrium without attention or fatigue. In locomotion, the flexors and extensors of the limbs are associated in a manner peculiar to each species of animal; and in man the balancing of the body, in progression, requires a still more extensive muscular combination than when at rest.

The spinal cord is not sufficient by itself for the acts of standing and locomotion; since a sudden lesion which deeply injures the brain or medulla oblongata, or the spinal cord above the cervical or lumbar enlargements, at once destroys the power of standing upright, or of making any effective movements of locomotion. In the frog, a very natural attitude is often preserved after decapitation, since the body rests by most of its under surface upon the ground; and this, through the reflex action of the spinal cord, brings the limbs underneath it in a flexed position. If such a frog be suspended in the air, the limbs hang down relaxed, but resume the attitude of flexion when placed in contact with a hard surface; and, according to Poincaré,* the frog can sometimes be made to execute a series of leaps, each concussion, as

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* Leçons sur la Physiologie du Système Nerveux. Paris, 1873, p. 72.

the body strikes the ground, giving a fresh stimulus for extension of the limbs. But in these animals, the muscular actions required for the attitude and locomotion are very simple. In warm-blooded quadrupeds and in man, on the other hand, they are more complex, and volition is essential for either standing or progression. Both these powers are consequently abolished by decapitation.

But, although the voluntary impulse is necessary for the acts of standing or walking, it is not concerned in the details of their mechanism. Once excited, the nervous action by which walking is accomplished may be kept up without mental effort or attention. All we have to do is to commence the process by an act of volition, and the requisite nervous machinery is set in motion. If we decide to turn a corner, all the muscular combinations necessary for that purpose are effected without the intermediate intervention of the will. This secondary action, by which motor impulses are combined in the movement of the limbs and trunk, is dependent on the action of the spinal cord.

The precise mode in which this is accomplished is not positively known. The most probable explanation is that it is due to a constant reflex activity of the cord, by which the muscles of the body and limbs are maintained in the proper degree of tension or relaxation; and that different parts of the cord are united with each other for this purpose by longitudinal fibres in the *posterior columns.*

According to this view, the fibres in question run a comparatively short course in the posterior columns, each one, after leaving the gray substance at one point, again entering it a few centimetres higher up; but, as they follow each other in continuous series, they form a mass of connecting strands throughout the cord. It is certain that at the borders of the gray substance and white columns of the cord there are fibres passing obliquely from one to the other; and this is especially true of the posterior columns and posterior horns. It is not possible, by any means of microscopic investigation now in use, to see the origin and termination of these fibres; but their existence is rendered probable by several well-established experimental and pathological facts.

I. The posterior columns of the cord, as shown by experiment, are not the channels for either sensibility or voluntary motion. But, according to Vulpian,* although a section of these columns at any one point produces no paralysis, in the ordinary sense, if they be divided by several transverse sections, two or three centimetres apart, there is a remarkable disturbance in the power of locomotion, like that which would be due to a want of muscular harmony.

II. Destructive lesions situated at any point in the spinal cord give rise to secondary degenerations like those already described (page 394), which are "ascending" or "descending" in various parts of its longitudinal columns. According to Charcot,† such secondary degenera-

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* Leçons sur la Physiologie du Système Nerveux. Paris, 1866, p. 381.

† Leçons sur les Localisations dans les Maladies du Cerveau et de la Moelle Epinière. Deuxième Partie. Paris, 1880, p. 243.

tions in the posterior columns are always ascending; that is, they extend from the primary lesion upward toward the brain, and never in a downward direction. But all parts of the posterior columns are not affected alike. The inner portion of these columns consists of a narrow band, next the median line, which throughout the cervical region is distinctly divided from the remainder by a narrow superficial furrow. This portion is known as the *funiculus gracilis*, or the "column of Goll." At the medulla oblongata it diverges from the median line, occupying on each side the inner border of the restiform bodies, and forming the so-called "posterior pyramids." These columns, in ascending degeneration of the spinal cord, are affected throughout their length, above the starting-point of the alteration, often quite to the level of the medulla oblongata (Fig. 108); and from this it is inferred that they consist mainly of fibres running continuously throughout.

FIG. 108.

TRANSVERSE SECTION OF THE SPINAL CORD; showing ascending degeneration of the columns of Goll, *G*, *G*. (Charcot.)

On the other hand, in the external portion of the posterior column, or that situated nearest the posterior horn of gray substance (Fig. 109), ascending degenerations extend only for two or three centimetres above their origin. It is therefore inferred that the longitudinal fibres in this part of the column have no great length, and that they originate successively from the gray substance, to terminate in it again soon afterward at a higher level.

III. Among the most important facts bearing on this question are those connected with the disease known as *locomotor ataxia*. In this affection there is a remarkable difficulty in walking, of such a character that the patient's natural gait is altered, and he is no longer sure of his movements. He loses the power of equilibrium, and cannot guide his foot to a particular point without a direct effort of the will. Consequently locomotion, as usually performed, becomes impossible; and yet the patient has not lost in any degree the power of voluntary movement, since he can often exert his full muscular force in grasping an object or in pushing or pulling with his legs or arms. But he has lost the power of involuntary muscular combination, which is essential for ordinary locomotion. For this reason the affection is called "ataxia," and not paralysis.

FIG. 109.

TRANSVERSE SECTION OF THE SPINAL CORD; showing Sclerosis of lateral portion of Posterior Columns. Locomotor Ataxia. (Charcot.)

In this disease the only parts of the nervous system invariably affected are the posterior columns of the spinal cord. They are the seat of a structural degeneration termed "sclerosis," in which the connective tissue is increased in quantity and density, while the nerve fibres are altered and atrophied. According to Brown-Séquard, if limited to a small extent of the posterior columns it does not usually affect the voluntary movements; but if it extend for a distance of several centimetres, in either the cervical or the dorso-lumbar region, it always causes a disturbance of these movements; and when it occupies the whole length and thickness of the posterior columns, the patient can neither stand nor walk, although while lying down and with the aid of vision he can still move his limbs in any direction.

But the sclerosis of the posterior columns producing locomotor ataxia is confined to their lateral portions. In this instance the disease is not a secondary degeneration, but a primary alteration of structure in the nervous tract, involving more or less completely its various parts. According to Charcot, degeneration or sclerosis of the columns of Goll (Fig. 108) never produces ataxia; while sclerosis of the lateral parts of the posterior columns (Fig. 109) is always accompanied by ataxic symptoms, and these symptoms are more marked on the right or left side or in the upper or lower limbs, according to the seat of the structural alteration.

These facts all point to the existence in the spinal cord of a power of reflex muscular coördination, dependent for its exercise on the longitudinal fibres of the posterior columns.

Another important action of the spinal cord, as a nervous centre, is its control over the *sphincters* and the *muscles of evacuation.*

While the small intestine, the cæcum, and the colon are supplied exclusively with nerves from the sympathetic system, the lower portion of the rectum receives branches from the sacral plexus of spinal nerves, distributed both to its mucous membrane and its muscular layer. The lower part of the large intestine is in great measure a temporary reservoir, in which the feces accumulate until the time arrives for their evacuation. The rectum, however, is in general nearly empty till shortly before evacuation; and when the feces begin to pass into it from above, it is still capable of retaining them for a certain period. Their retention and discharge are provided for by two sets of muscular fibres; namely, first, the sphincter ani, which keeps the orifice of the anus closed; and, secondly, the levator ani and the circular fibres of the rectum, which by their contraction open the anus and expel the feces. Both these acts are regulated by the reflex influence of the spinal cord.

In the normal condition, the sphincter ani is habitually contracted, thus preventing the escape of the contents of the intestine. An external irritation, applied to the verge of the anus, causes increased contraction and more complete occlusion of its orifice. This habitual closure of the sphincter, which is a purely involuntary act, as efficient during sleep as in the waking condition, depends on the reflex action of the spinal cord.

But when the rectum has become distended to a certain point, the nervous action changes. The impression then conveyed to the spinal cord causes relaxation of the sphincter ani. At the same time the levator ani draws the borders of the relaxed orifice upward and outward, and the feces are expelled by the muscular contraction of the rectum.

Both these actions are in some degree associated, during health, with sensation and volition. The distention of the rectum which precedes evacuation is accompanied by a sensation, and the resistance of the sphincter may be intentionally prolonged for a certain period. But this power of control is limited. After a time the involuntary impulse, growing more urgent with the increased distention, becomes irresistible; and the discharge finally takes place by reflex action of the spinal cord.

When the irritability of the cord is exaggerated by disease, its connection with the brain remaining entire, the distention of the rectum is announced by the usual sensation; but the impulse of evacuation is so urgent that it cannot be controlled, and must take place at once. The discharges are then said to be "involuntary."

If the cord, on the other hand, be disintegrated in its middle or upper portions, all sensibility and volition connected with the action of the sphincter are lost. The evacuation then takes place by the ordinary mechanism, as soon as the rectum is filled, but without the knowledge of the patient. The discharges are then "involuntary and unconscious."

Finally, if the lower portion of the cord, in an animal, be broken up by an instrument introduced into the spinal canal, the tonic contraction of the sphincter at once disappears. The same effect is produced, in man, by disorganization of the lower part of the spinal cord from injury or disease. The sphincter ani is then permanently relaxed, and the feces are evacuated without the knowledge of the patient, as fast as they descend into the rectum from the upper portions of the intestinal canal.

The *urinary bladder* serves also both as a reservoir and an organ of evacuation, its outlet being protected by the circular muscular fibres at the commencement of the urethra, known as the "sphincter vesicæ." While the nerves distributed to the kidneys are derived exclusively from the sympathetic system, those of the bladder consist partly of sympathetic filaments from the mesenteric ganglia, and partly of cerebro-spinal filaments from the lumbar portion of the spinal cord, both sets being united in the hypogastric plexus.

The tonic contraction of the vesical sphincter during health, by which the urine is retained in the bladder, is a continuous, involuntary, and unconscious act, like that of the sphincter ani. At the time of evacuation, the sphincter is relaxed by a voluntary impulse, and the muscular coat of the bladder contracts to expel its contents; but although the commencement of this process is voluntary, the subsequent contraction of the bladder continues independently of the will. According to the experiments of Giannuzzi* on dogs, irritation of the lumbar portion of the spinal cord, by pricking with a steel needle, causes con-

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* Journal de la Physiologie. Paris, 1863, tome vi., p. 22.

traction of the urinary bladder; but these contractions are no longer produced after dividing the roots of the sacral nerves. Irritation of either the sympathetic or the spinal nerve filaments going to the hypogastric plexus produces contraction of the bladder, more energetic in the latter case than in the former.

Disease or injury of the spinal cord causing complete paraplegia, is usually accompanied by paralysis of the urinary bladder. The muscular contraction of the bladder is therefore under the influence both of the sympathetic and cerebro-spinal systems; but its most energetic stimulus comes from the spinal cord through the sacral nerves.

The closure or relaxation of the sphincter vesicæ, on the other hand, is regulated by influences from the cerebro-spinal system alone. The resistance of the sphincter to the escape of fluid from the bladder, measured by Kupressow,* in the rabbit, was found equal to the pressure of a column of water more than 40 centimetres in height. That is, if in this animal one of the ureters were closed by a ligature, and an upright tube fastened in the other, the bladder and the upright tube might be filled with water to a height, on the average, of 44 centimetres without its escaping by the urethra; beyond that point the resistance of the sphincter was overcome, the water being discharged by the urethral orifice.

The experiments of Kupressow also show that the nervous centre of reflex action for the sphincter vesicæ is in the lumbar portion of the spinal cord. If the cord were divided at the level of the first or second lumbar vertebra, no difference was perceptible in the resistance of the sphincter; and sections at the third and fourth lumbar vertebræ diminished it by only two centimetres. But if the cord were divided at the fifth lumbar vertebra, the resistance was reduced to 14 centimetres; and the same effect was produced by section at the sixth and seventh vertebræ of the same region. The tonic contraction, therefore, of the sphincter vesicæ, although it may be aided by volition, is directly dependent on a nervous centre situated, in the rabbit, about the middle of the lumbar portion of the spinal cord; since it persists after the cord has been separated from the brain by a section at or above the fourth lumbar vertebra, but disappears after a section at or below the fifth lumbar vertebra, thus destroying the nervous centre or cutting off its communication with the bladder.

Both the retention of urine and its evacuation may be accomplished without the aid of volition. This is shown by the experiments of Goltz,† who found that after division of the spinal cord, in dogs, between the dorsal and lumbar regions, the animals, though deprived of sensibility and voluntary motion in the posterior limbs, could often retain their urine for a considerable time, and also evacuate it by a regular and forcible contraction of the bladder.

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* Archiv für die gesammte Physiologie. Bonn, 1872, Band v., p. 291.

† Archiv für die gesammte Physiologie. Bonn, 1874, Band viii., p. 474.

In man, when the sensibility of the bladder is exaggerated by inflammation, the reflex impulse to micturition is increased in intensity, producing an intolerance of urine. Under these circumstances the urine is discharged by a reflex act as soon as it has accumulated, in small quantity, in the bladder. The impression which excites this discharge is accompanied by sensation, but is too urgent to be resisted by the will.

On the other hand, injury of the spinal cord in the dorsal region may cut off all sensibility and voluntary power over the bladder, and yet the organ may be evacuated at regular intervals by the reflex action of the lumbar portion of the cord. But diseases or injuries which affect the cord in its lower portion, often produce complete paralysis of the bladder. The patient is consequently unable to discharge his urine in the ordinary way, and must be relieved by the introduction of a catheter. If this be not done, the urine accumulates; being retained for a time by the elastic tissues surrounding the neck of the bladder and urethra. But after distention has reached a certain point, this resistance is overcome; and the urine dribbles away from the urethra as fast as it is excreted by the kidneys. Paralysis of the bladder, accordingly, first causes distention of the organ, afterward followed by a continuous, passive, and incomplete discharge of its contents.

The spinal cord, in its character as a nervous centre, exerts a general protective influence over the body. It presides over the involuntary movements of the limbs and trunk; it supplies the requisite nervous connections for the attitude and locomotion; and by its control over the rectum and bladder, it regulates the accumulation and discharge of the excrementitious products of the system.

CHAPTER V.

THE BRAIN.

THE brain consists of various deposits of gray substance, and of tracts of white substance serving as commissures between its different regions, or as means of communication with the spinal cord. Its principal divisions are the cerebral hemispheres, the cerebellum, the tuber annulare, and the medulla oblongata. Of these the hemispheres are by far the largest; forming, in man, nearly four-fifths of the entire brain.

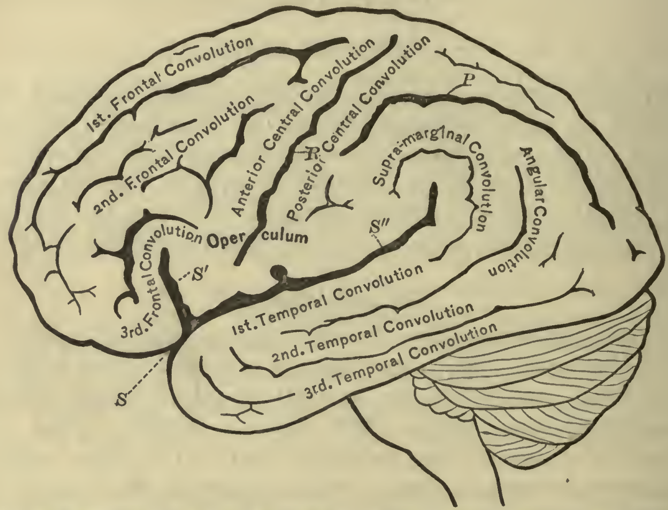
The Hemispheres.

The hemispheres are two ovoidal masses, flattened against each other at the median line, where they are separated by the great longitudinal fissure, and presenting on their lateral surfaces a rounded or hemispherical form, whence their name is derived. They consist externally of a layer of gray substance from two to three millimetres in thickness, covering a mass of white substance, the fibres of which in general radiate from within toward the cortical layer. Their surface is thrown into numerous convolutions, separated from each other by fissures generally from 10 to 25 millimetres deep. These fissures, like the great longitudinal fissure, are the spaces where opposite surfaces of adjacent convolutions lie in contact with each other; and they indicate the points at which the layer of gray substance folds inward, to return upon itself again and form the next convolution. The larger quantity of gray substance is, therefore, situated at the fissures rather than at the convolutions; and the more numerous and deeper the fissures on the surface of a brain, the greater the amount of gray substance which it contains.

Although the cerebral fissures and convolutions are not all the same in different brains, nor even exactly symmetrical in the two hemispheres, yet many of them are sufficiently constant to be regarded as essential features of the organ; and the remainder, while varying within certain limits, exhibit a general arrangement characteristic of the species to which they belong. In man they attain a very high degree of development; and their nomenclature is useful for designating different parts of the cerebral surface.

Next in importance to the great longitudinal fissure, which separates the hemispheres at the median line, is the *Fissure of Sylvius* (Fig. 110, S). This is a much deeper cleft than the others, and exists, according to Wilder, in all animals whose brains are fissured at all. In man it is the first to appear during embryonic life, being visible as early as the third month; and in the adult it forms a basis for the whole topographical division of the hemispheres. It commences as a transverse indentation on the under surface of the brain, running thence outward, backward, and upward, to form the anterior boundary of the temporal lobe. In some of the inferior animals all the convolutions on the convexity of the hemispheres follow the course of this fissure, bending round its upper extremity in a loop-like form; and in the human brain a similar general arrangement is distinctly visible.

Fig. 110.



Plan of the Human Brain, in Profile; showing its Fissures and Convolutions. S. Fissure of Sylvius; S′. Anterior Branch; S″. Posterior Branch; R. Fissure of Rolando; P. Parietal Fissure.

On the outer side of the cerebral hemisphere the fissure of Sylvius presents, in man, two distinct branches, namely, a shorter, anterior branch (S′), and a longer, posterior branch (S″). At its middle and anterior portions, the fissure is very deep, concealing beneath its folds a group of short radiating convolutions on the lower and lateral surface of the brain, called the "Island of Reil," or the *Insula.*

Externally the insula is covered by the convolutions included between the anterior and posterior branches of the fissure of Sylvius, which project downward from above and overlap, at this point, the deep-seated parts. This portion of the cortical mass is known as the "Operculum," or cover.

The second important fissure, on the convexity of the hemisphere, is the *Fissure of Rolando* (R). This fissure runs from near the median line outward and forward, reaching nearly to the fissure of Sylvius, and forming the boundary between the frontal and parietal portions of the hemisphere. It is bordered by two convolutions, running parallel with itself, namely, the "anterior and posterior central convolutions."

The third principal fissure is the *Parietal Fissure* (P). It starts from behind the posterior central convolution, and runs backward through the parietal portion of the hemisphere, curving downward toward its posterior extremity. Outside and below it are the arched convolutions about the fissure of Sylvius; inside and above it is a convolution running parallel with the great longitudinal fissure.

Beside the fissures just named there are five others, which, though less strongly marked, are constantly present and show considerable regularity in their position and arrangement. The first runs parallel with the fissure of Rolando, and a little in front of it; whence it is called the "præcentral fissure." The second runs through nearly the whole length of the frontal lobe, parallel in general direction with the great longitudinal fissure. It divides the upper from the middle portion of the frontal lobe, and is called the "superior frontal fissure." The third is the "inferior frontal fissure," and surrounds the end of the short anterior branch of the fissure of Sylvius. The two remaining fissures of this grade are situated in the temporal lobe, below and behind the fissure of Sylvius, with which they run in a general parallel direction.

The numerous remaining fissures, which increase to a great extent the convoluted aspect of the cerebral surface, are of secondary importance and irregular in location. Some of them run longitudinally along the middle of a convolution, dividing it into two narrower parallel folds; and some pass transversely between two fissures, across the intervening convolution. But if the arachnoid and pia mater be removed, these secondary fissures are found to be merely superficial indentations; not penetrating, like the others, deeply into the brain.

The principal convolutions on the convexity of the hemispheres are as follows:

The *First Frontal Convolution* runs from near the upper end of the fissure of Rolando, forward along the edge of the great longitudinal fissure to the anterior extremity of the frontal lobe, where it bends downward and backward, terminating below in a straight convolution next the median line, resting upon the upper surface of the orbital plate. This convolution is divided and folded in many ways by secondary transverse, oblique, and longitudinal fissures, but its general direction is easily recognized. It is bounded externally by the superior frontal fissure.

The *Second Frontal Convolution* runs parallel with the foregoing downward and forward over the anterior and lateral part of the frontal lobe. This is the widest of the three frontal convolutions, and the most abundantly variegated by secondary folds and fissures. It is separated from the first frontal convolution by the superior frontal fissure, and from the third by the inferior frontal fissure.

The *Third Frontal Convolution* is situated at the lower and outer part of the frontal lobe, and curves round the anterior branch of the fissure of Sylvius. It communicates posteriorly with the lower end of the anterior central convolution, and thus contributes to form the operculum.

The *Anterior Central Convolution* runs outward and forward from the great longitudinal fissure, along the front edge of the fissure of Rolando. It is usually a single convolution, but is more or less folded by transverse indentations. It communicates with the first frontal convolution above and with the third frontal convolution below. It also curves round the lower end of the fissure of Rolando, to unite with the following convolution, which may be considered as its continuation.

The *Posterior Central Convolution* is also parallel with the fissure of Rolando, but behind it. Above, it turns backward, uniting with the convolutions of the upper part of the parietal lobe.

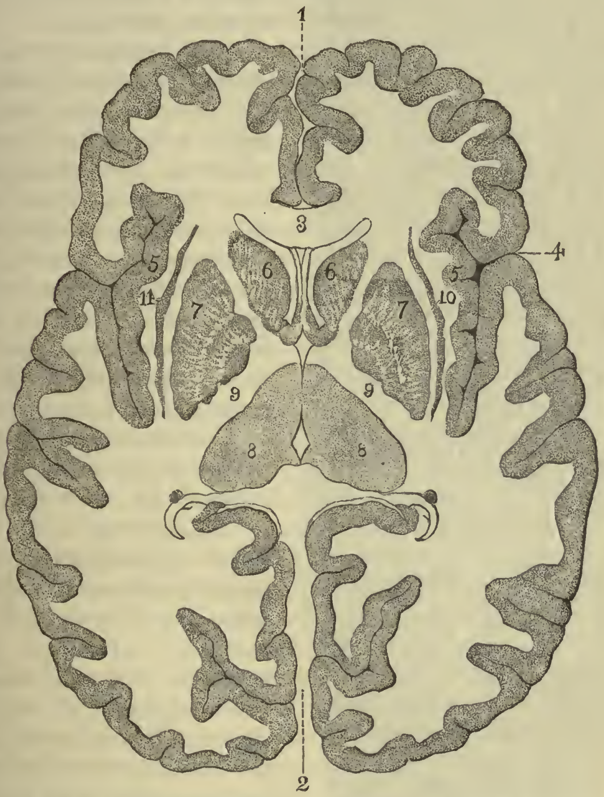
The *Supra-marginal Convolution* starts from the lower part of the posterior central convolution and arches round the upper end of the fissure of Sylvius. It then continues its curvilinear course, running downward and forward, parallel with the inferior margin of the fissure of Sylvius, toward the end of the temporal lobe. In this situation it is known as the *First Temporal Convolution.* It is usually divided throughout into two parallel convolutions by a secondary fissure running along its axis, and both these secondary convolutions are more or less transversely folded.

The *Angular Convolution* originates from the preceding and follows the inferior edge of the parietal fissure to its posterior extremity, where it makes a rather sharp turn downward and forward, whence its name of the "angular convolution." It then becomes continuous with the *Second Temporal Convolution* running downward and forward in the temporal lobe. Below this convolution, and parallel with it, is the *Third Temporal Convolution,* forming the inferior border of the temporal lobe.

In a horizontal section of the brain (Fig. 111), the convolutions are seen to penetrate its substance for varying distances at different regions. In the anterior and posterior parts they leave a comparatively thick layer of white substance between the cerebral ganglia and the gray matter of the cortex. But on the side of the brain, at the situation of the fissure of Sylvius, the convolutions reach to a greater depth. The cerebral ganglia are placed on each side the median line, near the base of the brain; the anterior pair, or the corpora striata, being separated from each other in front by the anterior horns of the lateral ventricles and the septum lucidum, and the posterior pair, or the optic thalami, being separated in a similar manner by the third ventricle except where they are united by the soft commissure and by the peduncles of the pineal body and the posterior commissure.

The corpora striata are penetrated from within and below by fibres, which run to a great extent in distinct bundles, thus producing a visible white striation in their gray substance. They form on each side, at their anterior and lowermost part, a continuous mass; but throughout their remainder they are divided by a narrow band of white substance into two portions, namely, the *caudate* nucleus (6), so called because it extends backward in a slender, curved, tail-like prolongation; and the *lenticular* nucleus (7), which has a somewhat lens-like figure, and is further divided into three concentric zones. Between the lenticular nucleus and the optic thalamus is a band of white substance, the *internal capsule* (9), consisting of fibrous bundles, the continuations of the crura cerebi, passing obliquely upward and outward from below. The optic thalamus (8), situated on the inner side of the internal capsule is of a lighter and more uniform tint than the corpus striatum, since the nerve fibres which penetrate it from below are dispersed in minute brush-like ramifications through its substance. On the outer aspect of the lenticular nucleus is a second envelope of white substance, known as the *external capsule* (10), with a thin layer of gray substance, the *claustrum*, or partition (11), and beyond that the white substance and convolutions of the *insula*

FIG. 111.



HORIZONTAL SECTION OF THE HEMISPHERES, AT THE LEVEL OF THE CEREBRAL GANGLIA.—1. Great longitudinal Fissure, between frontal lobes; 2. Great longitudinal Fissure, between occipital lobes; 3. Anterior part of Corpus Callosum; 4. Fissure of Sylvius; 5. Convolutions of the Insula; 6. Caudate Nucleus of Corpus Striatum; 7. Lenticular Nucleus of Corpus Striatum; 8. Optic Thalamus; 9. Internal Capsule; 10. External Capsule; 11. Claustrum.

(5). At this situation, accordingly, the gray substance of the cortex is in close proximity to that of the cerebral ganglia, while elsewhere it is separated from them by a considerable thickness of white substance.

FIG. 112.

VERTICAL SECTION OF ONE OF THE CEREBRAL CONVOLUTIONS; showing pyramidal cells, and bundles of fibres passing outward from the white substance. Magnified 300 diameters. (Henle.)

Gray Substance of the Convolutions.—The gray substance on the surface of the hemispheres forms a convoluted layer, into which the nerve fibres penetrate from the central mass of white substance. It consists of a uniformly granular matrix, in which are imbedded nerve cells and their prolongations, together with the nerve fibres dispersed among them. It is divided into several superimposed layers, distinguished by the form, size, and numbers of the nerve cells which they contain. The most characteristic of these elements are the so-called "pyramidal cells," occupying the middle portion of the gray substance. They have a pointed extremity, directed outward, while the base looks toward the white substance of the interior. The most superficial of these cells are the smallest and most numerous, averaging about 10 mmm. in diameter. Those which are more deeply seated are less abundant, but of larger size, from 25 to 40 mmm. in diameter. Some of the prolongations from the base of the cells lose themselves in the bundles of nerve fibres entering from the white substance.

Beneath the pyramidal cells is a layer containing much smaller cellular elements, from 8 to 10 mmm. in diameter, known as the "nuclear layer." Its cells have fine diverging processes, whose termination and connections are unknown.

As the bundles of nerve fibres penetrate the gray substance, they rapidly diminish in size, their fibres diverging laterally to pursue a more or less horizontal course; and in the external portions of the gray substance there are only isolated fibres running in various directions. During this dispersion, the nerve fibres become reduced to their smallest dimensions, measuring, according to Kölliker, from 1 to 2 mmm. in diameter. Most of them spread out at various levels in the gray substance, while others reach quite to its superficial portions.

Structure of the Gray Substance in Special Parts of the Hemispheres.—The gray substance of the convolutions presents certain peculiarities in particular regions, the most important of which are those described by Betz.* These observations, which were based on the examination of more than one thousand sections, show that there are differences of structure in the gray substance characteristic of extensive portions of the hemispheres. The cerebral surface is divided, in this respect, by the fissure of Rolando into two main departments, an anterior and a posterior. The anterior department, including the convexity of the frontal lobe, its under surface resting on the orbital plate, and its median surface at the great longitudinal fissure, is distinguished by the preponderance, in its gray substance, of the *layer of pyramidal cells.* In the posterior department, on the other hand, including both the occipital and temporal lobes, the nuclear layer predominates, the pyramidal cells being less abundant.

Furthermore, at the posterior border of each of these two departments there is a special region, characterized by cells of a particular variety. In front is the region of the so-called *giant pyramidal cells.* It occupies the whole of the anterior central convolution and the upper end of the posterior central convolution, and extends into the "paracentral lobule," which is a continuation of these two convolutions on the median surface of the hemisphere. The pyramidal cells in this region, as their name implies, are the largest in the brain, approximating and often equalling in size those of the anterior horns of gray substance in the spinal cord. They are from 40 to 60 mmm. in width, and from 50 to 120 mmm. in length. They all have a number of radiating processes, among which are two principal ones. One of them, given off from the point of the pyramidal cell, runs in a tapering and branching form toward the external surface of the convolution. The other, which is given off from the base of the cell and runs inward toward the white substance, is slender at its commencement, but soon grows thicker and acquires a medullary layer, assuming the appearance of a nerve fibre.

The posterior special region occupies the extremity of the occipital lobe. Its characteristic cells are of rather large size, but have few

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* Centralblatt für die medicinische Wissenschaften. Berlin, 1874. Nos. 37 and 38.

processes and no distinctly marked axis cylinder prolongation. Their terminal process is very slender and without lateral branches; while their basal processes extend mainly in a horizontal direction, and sometimes communicate with those of adjacent cells. These observations have been confirmed in many particulars by Tuke,* Lewis,† and Charcot,‡ and are generally accepted by cerebral anatomists.

Course of Fibres in the White Substance of the Hemispheres.—The white substance of the hemispheres consists mainly of nerve fibres or fibrous tracts belonging to three different orders, namely: 1st. Commissural fibres; 2d. Fibres of association; and 3d. Medullary fibres.

I. The *commissural fibres* are those which connect with each other similar parts of the right and left hemispheres. Their principal mass is in the "corpus callosum," or great transverse commissure of the cerebrum, which forms a broad band of white substance at the bottom of the longitudinal fissure and from which the constituent fibres spread out on each side to all the convolutions of the frontal and occipital lobes, and to the upper and posterior portions of the temporal lobe. Next in importance is the "anterior commissure," a narrow cylindrical band of white substance crossing the median line near the base of the brain, a little in front of the optic thalami, and whose fibres radiate on each side to the lower and anterior parts of the temporal lobe. This is accordingly a special transverse commissure for the convolutions situated below the fissure of Sylvius, while the corpus callosum is a general transverse commissure for those situated above, in front and behind it. By these commissural fibres the convolutions of each region of the hemisphere are placed in connection with those of the corresponding region on the opposite side.

II. The *fibres of association* form tracts lying immediately beneath the gray substance running in a general longitudinal direction, and connecting different convolutions on the same side. Many of them have a short course, connecting the gray substance of adjacent convolutions; others are longer, passing beneath one, two, or even three intermediate convolutions; while others run a very extended course, as from the point of the frontal lobe, along the edge of the longitudinal fissure to the end of the occipital lobe, or following the borders of the fissure of Sylvius to the end of the temporal lobe. According to Huguenin, it must be admitted that, in general, all the principal convolutions of a cerebral hemisphere are connected with each other by fibres of association, in longer or shorter tracts.

III. The *medullary* fibres are those which connect the hemispheres with the medulla oblongata. They come up from the spinal cord, through the medulla oblongata, and emerge from the superior border of the tuber annulare, as the crura cerebri. The crura cerebri are divided, about the middle of their thickness by a thin blackish gray

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* Edinburgh Medical Journal, 1875, vol. xx., p. 394.

† Brain. London, 1878, p. 79.

‡ Leçons sur les Localisations dans les Maladies du Cerveau. Paris, 1878, p. 34.

lamina, into two parts, a superior and an inferior. The inferior part, or that visible on the under surface of the brain, is called the "base" of the crura cerebri. It consists of two conspicuous diverging bundles, the fibres of which go to the corpora striata and internal capsule. The superior, deep-seated portion of the crura cerebri is called the "tegmentum" or cap. Its fibres pass to the optic thalami and internal capsule.

The internal capsule accordingly represents, on each side, the continuation of the crus cerebri. But this continuity is an interrupted one. The fibres forming the crus cerebri plunge, for the most part, directly into the corpus striatum in front and the optic thalamus behind, becoming dispersed in the gray substance of these ganglia, and, to all appearance, terminating in or among their nerve cells. These fibres, at the same time, are replaced by others which originate in the cerebral ganglia, and which, passing obliquely upward and outward, join the internal capsule, to continue their course toward the gray substance of the hemispheres. At the upper border of the ganglia, they spread out in the diverging bundles of the corona radiata, and thus reach, at last, the convolutions of the cortex. The internal capsule is accordingly composed partly of fibres which come up from the crura cerebri, and terminate in the cerebral ganglia, and partly of fibres which start from the ganglia, and run upward to the cortex; and the communication between the cerebral convolutions and the spinal cord is, for the greater part, an indirect communication through the cerebral ganglia.

Direct Medullary Fibres.—Beside the fibres above described, there is evidence that the internal capsule contains also tracts of direct communication, which pass through it from the convolutions to the crura cerebri without interruption by the gray substance of the ganglia. These direct fibres are of two kinds, namely; first, motor fibres, passing from the convolutions about the fissure of Rolando, through the middle part of the crura cerebri, to the pyramidal tracts of the spinal cord; and, secondly, sensitive fibres, passing from the spinal cord along the outer border of the crura cerebri, through the posterior part of the internal capsule toward the convolutions of the occipital lobe.

I. The direct motor fibres of the internal capsule have not been clearly demonstrated by methods of dissection; the intricate crossing in the upper part of the capsule making it difficult to follow individual fibres for a sufficient distance. Their existence is mainly inferred from the occurrence of *descending degenerations* in this part of the brain. According to Charcot,* destructive lesions of the cortical substance, in the anterior and posterior central convolutions, give rise to descending degenerations which pass through the internal capsule, crura cerebri, anterior pyramids, and lateral columns of the cord. Such

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* Leçons sur les Localisations dans les Maladies du Cerveau. Paris, 1878, pp. 156, 166.

descending degenerations take place without any accompanying lesion of the cerebral ganglia, and they are not produced by similar morbid alterations of the cortex in other parts of the brain. Instances of this kind, observed during a period of fifteen years, point to an immediate connection of certain fibres of the crus cerebri and internal capsule with the central convolutions of the cerebral hemispheres.

2d. The direct occipital fibres of the crus cerebri constitute a distinct tract on its external border, which turns outward beneath the extremity of the optic thalamus, and, forming the posterior part of the internal capsule, curves backward toward the occipital convolutions. This tract, which was described by Gratiolet,* from the dissection of brains hardened in alcohol, has been recognized by Meynert and Huguenin, and is generally admitted on anatomical grounds. Its existence, as well as the sensitive character of its fibres, is furthermore indicated by the fact that destructive injuries of the posterior part of the internal capsule, in which it is situated, produce loss of sensibility on the opposite side of the body.

Physiological Properties and Function of the Hemispheres.—The most important function belonging to the hemispheres, as a whole, is no doubt connected with the exercise of the intelligence. It is this part of the brain which is most developed in man as compared with the lower animals; and of all the nervous endowments it is the intellectual faculties in which he is most distinctly their superior. There are furthermore a number of special considerations which show that the cerebral hemispheres are in some way the especial organ of the mind.

I. It is certain in the first place that the hemispheres are not directly connected with the maintenance of physical life, and are not, even in man, essential to its continuance. They may be completely removed, on both sides, in fishes, reptiles, birds, and even in some mammalians, as the rabbit and the rat; and in the higher quadrupeds large portions of their substance may be destroyed, leaving all the vital functions in continued activity. In man they may suffer extensive morbid alterations or mechanical injuries, accompanied by loss of substance, without fatal result. One of the most marked instances of this kind is that reported by Bigelow,† in which a pointed iron bar, over one inch in thickness, was driven through a man's head by the premature blasting of a rock. The bar entered the left side of the face near the angle of the jaw, and passed obliquely upward, inside the zygomatic arch and through the anterior part of the cranial cavity, emerging from the frontal bone at the median line, just in front of the union of the coronal and sagittal sutures. The patient became delirious within two days after the accident, remaining partly delirious and partly comatose for about three weeks. He then began to improve, and at the end of rather more than two months from the date of the injury was able to

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* Anatomie Comparée du Système Nerveux. Paris, 1857, p. 186.

† American Journal of the Medical Sciences. Philadelphia, July, 1850.

walk. At the end of sixteen months the wounds were healed, and the patient had recovered his general health, though with loss of sight in the eye of the injured side. He survived for a little over twelve years, being able to do the work of an ostler, coachman, and farm-laborer, in all of which occupations he was employed at various intervals. The skull, deposited in the Warren Anatomical Museum,* shows the points of entrance and exit of the bar.

Other cases of severe injury to the hemispheres, which have been recorded from time to time, show that they do not take an important part in the immediate functions of life.

II. The results derived from comparative anatomy, and from extirpation of the hemispheres in animals, indicate that these organs are especially connected with the manifestations of conscious intelligence, as distinguished from involuntary, reflex, or instinctive actions. So far as we can appreciate the signs of intelligence in different species, they correspond in development with the hemispheres, rather than with any other portion of the encephalon. In many animals, muscular power and endurance, the activity of the special senses, and the promptitude of the instincts, are greater than in man; while in man, the intelligence is invariably superior to that of animals, and consequently gives him the advantage over them. Even among animals, that which especially characterizes certain species, and which most nearly resembles that of man, is a *teachable* intelligence; that is, one which understands the meaning of impressions received from the exterior, and thus enables its possessor, through the acquisition of new ideas, to profit by experience.

After complete removal of the hemispheres, in animals where this operation can be performed without danger to life, the general result is the loss of spontaneous action, and of the conscious adaptation of movements to external conditions; while the ability to perform instinctive and reflex movements is retained. In the pigeon, the standing posture is maintained without difficulty. The bird can usually rest with security upon a perch, and when forcibly dislodged will fly for a short distance and alight upon the ground in a nearly natural manner. But while undisturbed he remains in a state of profound quietude, with his eyes closed, and indifferent to surrounding objects. There is no spontaneous exercise of volition, but only such acts as are excited by the impressions of the moment. Occasionally he opens his eyes, stretches his neck, shakes his bill once or twice, or smooths the feathers upon his shoulders, immediately relapsing into his former condition of apathy.

But there are still indications of both general and special sensibility. If the foot be pinched with a pair of forceps, the bird becomes partially roused and moves once or twice from side to side. Vulpian has seen a pigeon within a short time after the operation shake the

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* Descriptive Catalogue of the Warren Anatomical Museum. Boston, 1870, p. 145.

head briskly in consequence of a fly having alighted on the wound. The discharge of a pistol behind his back will often cause him to open his eyes and turn his head, as if in sign of having heard the report; but he immediately becomes quiet again and pays it no further attention. Vulpian found that in a pigeon, after the animal had been roused by pinching the foot, the sudden approach of a hand toward the eye caused a winking movement with partial turning of the head. Sometimes such a pigeon will fix his eye on a particular object for several seconds together; and Longet found that on moving a lighted candle before the bird in a dark place, its head would often follow the movements, showing that the retina was still sensitive to light.

But it is doubtful whether such movements indicate a real perception on the part of the animal, or whether they are simply automatic reactions of the nervous system, like the contraction and dilatation of the pupil in a person who is unconscious. It is certain that, if impressions are perceived by the pigeon after removal of the hemispheres, they are immediately forgotten; and furthermore that they do not excite any corresponding series of ideas. The report of a pistol causes no sign of alarm, and is not followed by any attempt at escape; for the sound, even if perceived by the animal, does not suggest any idea of danger or injury. External phenomena, and their impressions on the nervous system, are without significance for the animal; and he is consequently no longer capable of originating intelligent volitional acts.

III. In man, the general result of injury or disease of the hemispheres is a disturbance of the intellectual faculties. Among the earliest and most constant of these phenomena is an impairment of memory. The patient forgets the names of particular objects or persons; or he is unable to calculate numbers with his usual facility. His mental derangement is often shown in the undue estimate which he forms of passing events. He will show an exaggerated degree of solicitude about a trivial occurrence, while he pays no attention to matters of real importance. As the difficulty increases, he becomes careless of directions and advice, and must be managed like a child or an imbecile. Finally, when the injury to the hemispheres is excessive, the senses may still remain impressible, while the patient is completely deprived of intelligence. The frequency of these results in lesions of the hemispheres, without loss of sensibility or motion, shows the close connection between the mental powers and the nervous action of this portion of the brain.

The same connection is seen in congenital idiocy with imperfect development of the brain. In many cases the immediate condition upon which idiocy depends is the small size of the brain as a whole, and particularly that of the cerebral hemispheres. The general and special senses, and the activity of the nervous system at large, are sometimes fully developed in idiots, while the intelligence remains at so low a grade, that no improvement in the mental operations is possible, and instruction is consequently without effect.

The mental endowments chiefly concerned in the manifestations of intelligence are memory, reason, and judgment.

Memory is the simplest and most essential of these faculties for the performance of intelligent acts. The recollection of names, and of the objects to which they belong, is indispensable for even the use of articulate language; and a defective memory often seems the immediate cause of the incapacity of idiotic children. Memory is constantly essential in the ordinary occupations of life, in enabling us to retain past impressions as a guide for immediate or future acts.

Reason may be considered as the ability to appreciate the nature of nervous impressions, and to refer them to their external source. This is quite different from the simple power of perception, which may continue unimpaired after extensive injury of the hemispheres. The mental action excited by an impression on the senses transfers our attention from the sensation to its cause; and when this action is prompt and effectual, we acquire an idea both of the origin of the impression and its significance. The perfection of this quality consists in the certainty with which it appreciates the relation between cause and effect and the relative importance of different phenomena. It is deficient or absent in idiots, and they consequently cannot avoid dangers, or provide for their necessities. For the same reason it is useless to punish an idiot, because, although he may feel the pain inflicted, he does not refer it as a consequence to any previous act of his own. A similar deficiency in the insane or the weak-minded produces a want of power to comprehend the importance and connection of different events. They are said to be "unreasonable," because they expect results which are unlikely to follow from certain causes, and because they assume the existence of causes which are not indicated by the results.

Judgment is the faculty by which appropriate means are selected for the accomplishment of a particular end. Its exercise requires the existence of reason and memory, which supply the necessary conditions upon which it is based; while its own action is one which looks to the future rather than to the past. An individual in whom the judgment is well developed employs, under the guidance of experience, means which are adapted to the end in view; one who is deficient in this respect resorts to means which are insufficient or inappropriate, and is consequently unsuccessful. Whether the act performed in this manner be a simple mechanical operation, like that of shutting a door to exclude the cold, or a complicated plan involving many parts, the mental process is the same in kind, and differs only in degree; its essential character being that it is an intelligent act, based on an understanding of the previous conditions, and intended to accomplish a definite result.

It is evident that all such manifestations of intelligence are in the nature of reflex actions. Their starting point is a sensation coming from without, giving rise in the nervous system to a series of internal operations, and terminating in an intelligent volitional impulse. This is reflected from within outward, and thus finally calls into action the voluntary muscles. The intermediate process, between the sensation and the volition, may be short and simple; or it may be long and complicated, involving the continued suggestion of many successive ideas. There can be little doubt that, in either case, it is accompanied by actions of some kind in the gray substance of the cerebral hemispheres; for if these organs are injured or defective, the mental operations are obstructed or disturbed.

But the nature of the nervous process accompanying mental action is unknown. Physiological research gives us no information with regard to the brain as an organ of intelligence, beyond the fact that it is, in some way, essential to its manifestation; and all the modern investigations into its structure and physiological properties have failed to increase, in any essential particular, our knowledge of its office and action in the operations of the mind.

Localization of Function in different parts of the Hemispheres.— On the other hand, the most valuable information has been obtained of late years from the study of the simpler nervous functions and their localization in different parts of the hemispheres. The recent improvements in our knowledge of cerebral physiology relate almost entirely to the brain as an organ for combining and regulating the nervous mechanism of conscious sensations and voluntary movements. They show that certain parts of the cortex of the hemispheres are connected with phenomena of motion, others with the power of sensation; while others still, so far as yet known, are indifferent to both these functions, and are perhaps connected with nervous acts of a different kind. The hemispheres, accordingly, do not act indiscriminately as a whole; but the convolutions of particular regions have a structure and properties differing from those elsewhere. The knowledge thus far obtained relates chiefly to three different points, namely, 1st. Centres of Motion; 2d. Centres of Sensation; 3d. The Centre of Language.

I. The beginning of the present doctrine on this subject was the discovery, by Fritsch and Hitzig* in 1870, of the centres of motion in the hemispheres of the dog. They showed that galvanic currents, of low intensity, applied to certain points on the surface of the convolutions, give rise to definite movements of the head, body, or limbs; while no such effect is produced by galvanization of the cerebral surface in other regions. These experiments were subsequently extended to cats, guinea-pigs, rabbits, and monkeys. They have been confirmed by many other observers in England, France, Italy, and the United States, and we have repeatedly verified their main results.†

The important features of these experiments are as follows. When the animal is etherized, and the convexity of the hemisphere exposed on one side by trephining the skull, the poles of a galvanic battery, applied to many parts of the convoluted surface, produce no visible

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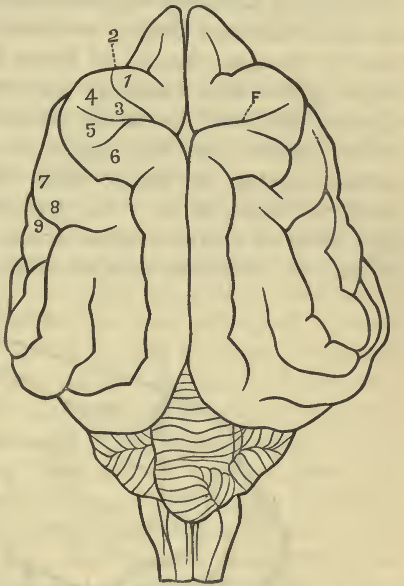
*Archiv für Anatomie, Physiologie und wissenschaftliche Medicin. Leipzig, 1870, p. 300. Hitzig, Untersuchungen über das Gehirn. Berlin, 1874.

† New York Medical Journal, March, 1875, p. 225.

result. But at certain circumscribed localities, the application of the galvanic stimulus causes definite movements of the limbs, head, or trunk. These movements always take place on the opposite side of the body. They are different from the general convulsive reactions produced by galvanizing the spinal cord, the trunk of a spinal nerve, or the base of the brain. They are confined to particular muscles or groups of muscles, and produce flexion or extension of the anterior or posterior limb separately, or of a single joint in either. They are not quite instantaneous, but often have a certain appearance of deliberation, and resemble in character the normal voluntary movements in a waking condition. In the same animal, particular movements, such as flexion or extension of the fore or hind paw, always follow galvanization of particular points on the cerebral convolutions, the relation between the spot galvanized and the part moved remaining invariable. The spot on the cerebral surface which thus responds to galvanization by the movement of a particular limb or part of a limb is therefore called the "centre of motion" for that part. In different dogs the special centres of motion are not strictly identical in locality, but they are very nearly so; and the region within which these centres exist, or the "motor region," is as definitely marked as any other anatomical division of the brain. It comprises chiefly the convolutions surrounding the so-called "frontal fissure," a nearly transverse furrow in the anterior portion of the dog's brain, running outward for a short distance from the great longitudinal fissure.

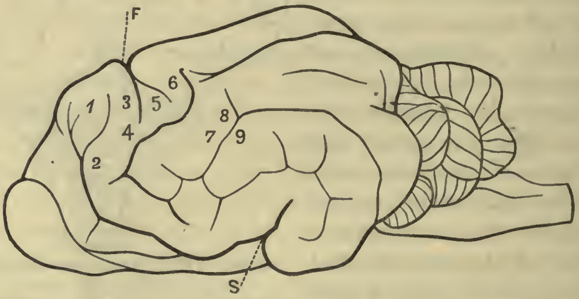
Fig. 113.



Brain of the Dog, from above; showing centres of motion in the convolutions. F. Frontal fissure. 1. Flexion of head on neck, in the median line. 2. Flexion of head on neck, with rotation toward the side of the stimulus. 3, 4. Flexion and extension of anterior limb. 5, 6. Flexion and extension of posterior limb. 7, 8, 9. Contraction of orbicularis oculi and other facial muscles.

It was for some time a matter of doubt whether the localized movements in question were produced by stimulation of the cortex, or whether they were due to a diffusion of the galvanic current and consequent irritation of more deeply-seated parts, especially the corpora striata. But this doubt is no longer entertained by the majority of physiologists. When the distance between the two electrodes, and therefore the length of the current traversing the convolution, is only one millimetre, galvanization of a particular spot may produce, many times in succession, a definite muscular contraction; and yet the application of the electrodes to neighboring spots, not more than five millimetres distant from the first and equally near the base of the brain, may be without effect. Ferrier* has found, in experiments on monkeys, that stimulation of the convolutions of the insula, which lie in close proximity to the corpus striatum, produces no visible result; while that of the more distant convolutions in the motor region on the surface of the hemisphere causes an immediate and definite movement. Lastly, decisive proof is supplied by the experiments of Braun† and Putnam.‡ In these experiments points were found on the cerebral convolutions where electric stimulus produced the usual definite muscular contractions. A horizontal section was then made one or two millimetres beneath the surface, leaving the flap in place but cutting off the anatomical continuity of brain tissue. The irritation, then reapplied to the original spot, failed to excite muscular contraction; but if the flap were turned up and the electrodes applied to the cut surface beneath, a current of similar or slightly increased strength produced the same movements as before. Repeated trials of this kind, the flap being alternately removed and readjusted, yielded the same results. It is evident, therefore, that when the electrodes, applied to the surface of the uninjured brain, cause movements on the opposite side of the body, this is due not to a diffusion of the electric current toward the base of the brain, but to a nervous stimulus originating in the convolutions, and thence transmitted by the fibres of the white substance.

FIG. 114.



BRAIN OF THE DOG; profile view, showing centres of motion in the convolutions. F. Frontal fissure. S. Fissure of Sylvius. 1. Flexion of head on neck, in the median line. 2. Flexion of head on neck, with rotation toward the side of the stimulus. 3, 4. Flexion and extension of anterior limb. 5, 6. Flexion and extension of posterior limb. 7, 8, 9. Contraction of orbicularis oculi and other facial muscles.

The reality of the motor centres in the cerebral convolutions is corroborated by other important facts of two kinds.

First. The cortical substance of the region in question has a special

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* The Localization of Cerebral Disease. London, 1879, p. 17.

† Centralblatt für die medicinischen Wissenschaften. Berlin, June 13, 1874, p. 455.

‡ Boston Medical and Surgical Journal, July 16, 1874.

anatomical structure, which distinguishes it from other parts of the hemispheres. In the investigations of Betz, already quoted (page 419), it was found that in the brain of the dog the motor region about the frontal fissure was that which contained in its gray substance the "giant pyramidal cells," similar in size to the cells of the anterior horns in the spinal cord, and exclusively existing in the cortical layer of this part of the brain. The microscopic structure of these convolutions has therefore an individual character, corresponding with their physiological properties.

Secondly. Extirpation of the motor centres in the cerebral convolutions produces more or less paralysis of voluntary motion on the opposite side of the body. This has been shown in experiments on dogs by Hitzig, Schiff, Hermann, and Carville and Duret.*

The paralysis affects special movements, according to the particular seat of the lesion; and when a certain spot on the cerebral convolutions has been found by stimulation to excite movements of flexion or extension in one of the opposite limbs, its extirpation causes paralysis of the same movement. But the paralysis thus produced varies in extent and duration in different animals. In the pigeon, removal of an entire hemisphere hardly interferes with the acts of standing or locomotion. In the dog, destruction of the motor centres on one side causes a partial hemiplegia, which has a distinct effect on locomotion, but which after some days or weeks gradually disappears, the animal recovering his natural power of movement. In the monkey, according to Ferrier, the hemiplegia from this cause is strongly marked, and shows no indication of amendment; while in man, according to numerous pathological observations, it is absolutely complete and permanent.

This difference is explained by supposing that in the lower animals the movement of the limbs in locomotion is mainly confined to consentaneous acts, in which direct volition takes a small share; while in the higher animals, and especially in man, the influence of immediate volitional impulses is more essential, and preponderates in importance, according to the number and variety of the muscular actions.

In man, the motor region of the cerebral hemispheres comprises in general terms *the convolutions about the fissure of Rolando*, and especially the anterior and posterior central convolutions. It would hardly be possible to assume this from the analogies of external configuration, since the comparative size of the hemispheres and the proportion of their various parts differ so widely in the dog's brain and that of man; but it is made certain by anatomical and experimental facts, as well as by the result of observation in disease. In man it is the convolutions surrounding the fissure of Rolando which present, like those of the motor region in the dog's brain, the special structure characterized by the presence of "giant pyramidal cells," which are not found elsewhere.

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* Archives de Physiologie. Paris, 1875, 2me série, tome ii., p. 352.

Furthermore, in the experiments on the monkey by Ferrier,* which have given to this subject a great extension, the motor centres were found to occupy a similar region. In this animal the general form of the hemispheres is so similar to that in man that the principal fissures and convolutions can be recognized without difficulty; and by stimulating various points of the anterior and posterior central convolutions, with others more or less closely adjacent, the same kind of definite movements are produced as in the dog by stimulation of the motor region.

Lastly, in man, there is now a large body of evidence to the same effect. It consists of numerous cases observed or reported by Charcot,† Ferrier,‡ Rendu,§ and Grasset,‖ in which there were local epileptiform convulsions on one side coexisting with irritation of the opposite central convolutions, or hemiplegia caused by their disorganization. According to Rendu, local lesions of small extent, when seated in the motor region, produce hemiplegia; while others of large area, sometimes occupying nearly a whole lobe, if outside this region, are not accompanied by paralysis. The hemiplegia in man, resulting from disorganization of the cortex in the motor region, is complete and permanent, and is not associated with any loss of sensibility.

II. The *centres of sensation* in the cortex of the brain have not been localized to the same extent nor with the same certainty as the centres of motion. There is reason to believe that the power of perception for sensitive impressions in general has its seat in some part of the cerebral cortex, and that it is located in the posterior region of the hemispheres; since a loss of sensibility on the opposite side of the body, both in the higher animals and in man, is produced by lesions of the posterior part of the internal capsule. According to the experiments of Flourens,¶ all distinct perception, both general and special, disappears in the pigeon after removal of both hemispheres; and after removal of a single hemisphere sight is abolished in the eye of the opposite side.

The power of visual perception is especially located by Ferrier** in the angular convolution. This observer found that, in the dog, the cat, and the monkey, electrical stimulation of this convolution caused rotation of the eyeballs and sometimes turning of the head toward the opposite side, with contraction of the pupils, as if from a visual sensation; and in the monkey destructive lesions of the angular convolution produced blindness of the opposite eye, while vision remained in the

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* Functions of the Brain. London, 1876.

† Leçons sur les Localisations dans les Maladies du Cerveau. Paris, 1878, p. 166.

‡ The Localization of Cerebral Disease. London, 1879, p. 42.

§ Revue des Sciences Médicales. Paris, 1879, tome xiii., p. 314.

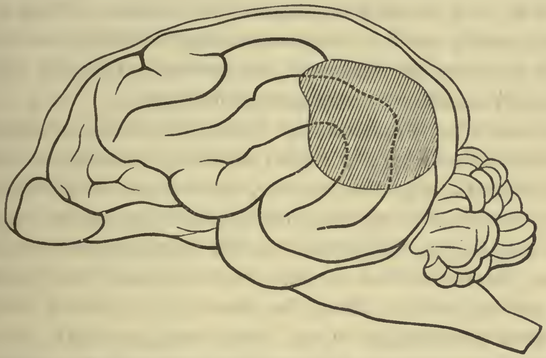
‖ Des Localisations dans les Maladies Cérébrales. Paris, 1880, p. 143.

¶ Recherches Experimentales sur les Propriétés et les Fonctions du Système Nerveux. Paris, 1842, pp. 31, 123.

** Functions of the Brain. London, 1876, p. 180.

eye of the same side. After unilateral destruction of the angular convolution, vision returned to some extent in the blinded eye after twenty-four hours; but if the convolution were destroyed on both sides, blindness was complete, and there was no return of sight in either eye. The operation produced no other effect than loss of vision; general sensibility and the power of motion being unimpaired.

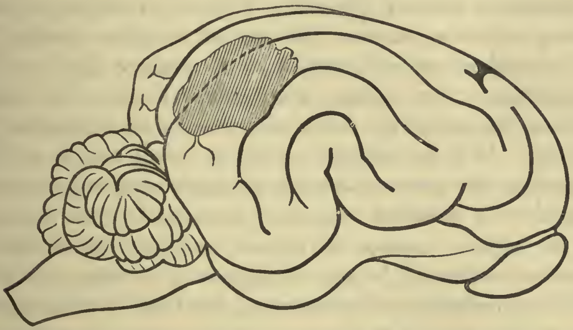
Fig. 115.



Brain of Dog; showing excision of angular convolution and two adjacent anterior convolutions on left side. Blindness of right eye.

We have obtained similar results in the dog by excision of the angular convolution on the right and left sides in two different animals.

Fig. 116.



Brain of Dog; showing excision of angular convolution and adjacent posterior convolution on right side. Blindness of left eye.

In each case vision remained perfect in the eye of the same side with the injury, but was abolished in the eye of the opposite side. There was no other perceptible affection of either sensibility or movement; and the blindness of the affected eye was persistent during the life of the animal, continuing in one instance for over ten days. It appears accordingly highly probable that the power of visual perception is seated in that part of the cortex occupied by the angular convolution.

III. There is at present no doubt as to the existence in the cerebral cortex of a *centre of language*—that is, of a region which, in man, presides over the necessary combinations for articulate speech. Many animals have the power of communicating with each other by certain movements and sounds in such a way as to attract attention, and enable them to act in concert. The language thus employed is a language of expression, and consists in such modifications of the tone of voice or position of the limbs as indicate pleasure or dislike, excitement or alarm, or a friendly or hostile disposition. In man the same methods are largely used to express similar feelings, and to represent others, such as surprise, contempt, amusement, or doubt, which do not seem to exist in animals to an appreciable degree.

But man has also the faculty of conveying definite information by means of articulate speech, in which arbitrary sounds are used to indicate special objects, qualities, or acts, as well as the relations between them. The power of using articulate language for the expression of thought is usually in proportion to the development of the general intelligence. In order that it may be exercised, two faculties must come into action, namely, first, the memory, by which the particular words required are brought to the mind; and, secondly, the voluntary combination of movements necessary for articulation. These acts are performed, in health, with such rapidity that we are not conscious of them; and articulate speech seems to be a direct sequence of our internal ideas. But pathological cases show that either one or both of the above faculties may be absent, while the ideas and the desire to express them are as distinct as ever.

This affection is termed *aphasia.* It does not depend upon a want or confusion of ideas, because the patient is often perfectly clear as to what he wishes to say, although he cannot say it. It is not due to paralysis of the organs of articulation, since the tongue, lips, and palate can be moved for other purposes, in any direction, with the usual facility. It is an inability either to recall the word needed, or to set in motion the nervous actions required to pronounce it. In the former instance it is called "amnesic aphasia." The patient cannot say what he wishes, because he cannot recollect the word he wants. For the same reason he is also incapable of writing it. But if the word which he requires be pronounced for him, he recognizes it, and can repeat it, though in a few seconds it has again escaped him. This disease is an aggravated form of the condition to which many otherwise healthy persons are liable, namely, that of sometimes forgetting a particular word at the moment it is required for use. In some cases of aphasia the loss of power is so complete that the patient can utter only two or three words, which he employs indiscriminately on all occasions.

In the second variety of the affection the patient knows the word he wants, but cannot articulate it. He can, therefore, express himself perfectly well by writing, but is unable to read aloud even what he has written. This is called "ataxic aphasia," because it depends upon a defect of nervous combination.

Observations on the locality of the centre of language tend to place it more especially in the *convolutions surrounding the lower end of the fissure of Sylvius, and in those of the insula.* Broca refers it to the posterior part of the third frontal convolution, while others consider it as belonging to the frontal lobe in general. The evidence for this localization consists in a number of instances in which aphasia has been found, on post-mortem examination, to be accompanied by lesions of the brain confined to the points indicated. It is often accompanied by hemiplegia, but may exist independently of any paralytic affection.

According to the majority of observers, the nervous centre for articulate speech is seated upon one side of the brain only, and, as a rule, in the *left hemisphere.* This conclusion is derived from the large preponderance of cases in which aphasia is associated with hemiplegia on the right side of the body rather than on the left. It is still more strongly corroborated by such instances as that reported by Bateman,* of chronic left hemiplegia without aphasia, followed in the same individual by a sudden attack of right hemiplegia with aphasia. It is not supposed that the two hemispheres are absolutely different from each other in this respect; but that the functional superiority of the left side, in the production of language, is like that by which we are enabled to use the right hand for certain delicate manipulations of which the left is incapable. A lesion of the motor centres in the right hemisphere would paralyze only the ordinary movements effected by the left hand; but a lesion of the same extent in the left hemisphere would further paralyze the special movements, like writing or drawing, for which we depend on the right hand. It is, perhaps, for a similar reason that a patient with destructive injury of the left hemisphere becomes incapable of language, while one with a corresponding injury on the right side is not affected in the same way. This would also explain the exceptional cases in which aphasia coincides with left hemiplegia; just as certain individuals are habitually left-handed, and would consequently be rendered incapable of delicate manipulations by hemiplegia of the left side.

Hemiplegia and Hemianæsthesia from Cerebral Lesions.—It has already been shown that hemiplegia of the opposite side of the body, without alteration of sensibility, results, in man, from destructive lesions of the cerebral convolutions in the motor region. It is also known that hemianæsthesia, or loss of sensibility in one lateral half of the body, may take place, without paralysis of motion, from cerebral disease. Both these affections may furthermore be produced by lesions limited to particular parts of the white substance. This substance consists of tracts connecting the cortical convolutions, through the corona radiata and internal capsule, with the base of the brain, and

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* On Aphasia. London, 1870, p. 152.

finally with the peripheral organs. If these tracts be injured in any part of their course, hemiplegia, hemianæsthesia, or both, may follow as a consequence.

The locality of lesions producing *hemiplegia* is in the anterior portion of the internal capsule. In the experiments on dogs by Carville and Duret,* section of the internal capsule in this region, between the caudate nucleus and the lenticular nucleus, was constantly followed by hemiplegia of the opposite side of the body. In man, the results of pathological observation are to the same effect. According to Charcot,† although destructive lesions, limited to the gray substance of the corpus striatum or optic thalamus, may produce symptoms of hemiplegia, the paralysis in these instances is usually incomplete and transitory: and is often to be referred, in cases of hemorrhagic effusion, to temporary compression of the internal capsule. On the other hand, lesions confined to the internal capsule, in its anterior two-thirds, produce an opposite hemiplegia which is strongly marked and persistent, and usually unaccompanied by any loss of sensibility. The destruction of continuity in the fibres of the internal capsule from such injuries is final, and the resulting paralysis is consequently permanent.

The production of *hemianæsthesia* from lesions of the internal capsule is limited, in an analogous way, to its posterior portion. The region of cortical substance devoted to the perception of tactile sensations has not been determined to the general satisfaction of physiologists. But there is reason to believe that it is seated somewhere in the posterior portion of the hemisphere; and there is no question that the communicating tracts of centripetal fibres, subservient to this function, are in the hinder part of the internal capsule. The extreme posterior border of this capsule is formed by the direct sensitive fibres from the outer part of the crura cerebri already mentioned (page 422) as described by Gratiolet. In the experiments of Veyssière‡ on dogs, it was shown that for the production of persistent hemianæsthesia from cerebral lesions, it was indispensable that the injury involve the fibres of the internal capsule.

According to the researches of Carville and Duret, already quoted, it appears that while a destructive injury in the anterior portion of the internal capsule causes hemiplegia without hemianæsthesia, a lesion of its posterior portion is followed by hemianæsthesia without hemiplegia. In each case the morbid effects are produced on the opposite side of the body. The same rule holds good in man. According to Charcot, the question whether a lesion in the neighborhood of the cerebral ganglia shall produce loss of motion or loss of sensibility depends on which part of the internal capsule it involves. If seated in the anterior two-thirds it produces hemiplegia; if in the posterior third, it is a hemi-

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* Archives de Physiologie. Paris, 1875, 2me série, tome ii., p. 352.

† Leçons sur les Localisations dans les Maladies du Cerveau. Paris, 1878, pp. 96, 98, 99, 100.

‡ Hémianæsthésie de Cause Cérébrale. Paris, 1874, p. 73.

anæsthesia which results. Hemianæsthesia of cerebral origin, according to the same observer, is characterized by the fact that, together with loss of sensibility in the body and limbs, there is a similar insensibility in the integument of the head and face, and in addition a loss or impairment of the special senses; taste, smell, hearing, and vision being all more or less affected, on the side opposite to that of the cerebral lesion. This will serve to distinguish hemianæsthesia due to injury of the brain from that caused by a lesion of the spinal cord, in which the only symptom present is loss of sensibility on one side of the body.

The Cerebellum.

The cerebellum, though much inferior in size to the cerebrum, consists, like it, of a folded cortical gray layer surrounding a central mass of white substance. The cortical layer is only about one-half as thick as that of the cerebrum; being nowhere over 1.5 millimetre in thickness. But its convolutions are very compactly arranged in the form of thin, closely adjacent laminæ; so that it contains a comparatively large quantity of gray substance.

The cortical layer of the cerebellar convolutions is penetrated by fibres from the interior white substance, and contains nerve cells of various form and size. The most characteristic are flask-shaped cells, arranged in a single or double row; the rounded extremity of each cell being directed inward, the pointed extremity outward. According to Kölliker and Henle, the cells usually give off prolongations in two opposite directions; that which passes inward toward the white substance being unbranched and resembling the axis-cylinder of a nerve fibre, while that which passes toward the surface of the convolution divides into numerous ramifications.

The cerebellum is connected with the rest of the cerebro-spinal axis, 1st, by the inferior peduncles, or *restiform bodies*, which come from the posterior and lateral parts of the medulla oblongata, to radiate in its white substance; and 2d, by the superior peduncles, or *processus e cerebello ad corpora quadrigemina*, which originate from the cerebellum nearer the median line than the restiform bodies, and thence pass upward and forward, joining the longitudinal tracts of the tuber annulare and crura cerebri. 3d, The two lateral halves of the cerebellum are furthermore connected with each other by the middle peduncles, which originate from the white substance on each side, and pass forward and downward to meet in front upon the under surface of the tuber annulare, forming the arched commissure of the *pons Varolii.*

Physiological Properties of the Cerebellum.—The general result of experimental operations on the cerebellum shows that the surface of this organ is inexcitable by ordinary means, and that its mechanical irritation gives no evidence of sensibility. Flourens, Longet, Vulpian, and experimenters in general, have recognized the fact that neither sensation nor muscular contractions are produced by touching or wounding its external gray substance; while in its deeper portions both excitability and sensibility become manifest, in proportion as the irritation is applied nearer the medulla oblongata and the inferior peduncles. Furthermore, its removal, either in part or in whole, does not essentially diminish either sensation or the power of movement. The senses remain active, and the intelligence is unimpaired, provided the cerebral hemispheres are intact. If injury of other adjacent parts be avoided, the cerebellum may be extensively wounded or even totally removed in many animals without causing death. One-half or two-thirds of its substance have often been taken away in the pigeon; and in one of the experiments of Flourens, a fowl lived for more than four months after its complete extirpation.

Aside from these particulars, experiments consisting in mutilation or removal of the cerebellum have yielded very uniform and striking results, quite different from those caused by injury to other parts of the brain. These effects were first described by Flourens,* and notwithstanding the great activity of research since that time, his results have been corroborated in all essential particulars by subsequent observers. They have been witnessed, by different observers, in the pigeon, fowl, duck, turkey, and other birds; and, among quadrupeds, in the dog, the cat, the mole, the rat, and the guinea-pig.

The effect produced by partial or complete destruction of the cerebellum is a peculiar disorder of movement in the body and limbs, from want of harmony in their muscular action. The power of associating different muscles, in such a way as to produce coördinated movements, is impaired in proportion to the extent of injury to the nervous centre. In the pigeon, if a small portion only of the cerebellum be removed, the animal exhibits a peculiar uncertainty in the gait, and in the movement of the wings. If the injury be more extensive, the power of flight is lost and the bird can walk, or even stand, only with difficulty. There is no actual paralysis, for the movements of the limbs are often rapid and energetic; but there is a want of control over the muscular contractions, similar to that shown by a man in a state of intoxication. The movements are confused and blundering; so that the animal cannot direct his steps to any particular spot, nor support himself in the air by flight. He reels and tumbles, but can neither walk nor fly.

The senses and the intelligence are at the same time unaffected, and this causes a striking difference between the effects produced by removal of the cerebrum and that of the cerebellum. If these operations be done upon two different pigeons, the animal from which the cerebrum only has been removed will remain standing upon his feet, in a condition of complete repose; while the other, from which the cerebellum has been taken away, is in a constant state of agitation, frequently endeavoring, with violent and ineffectual struggles, to perform movements which he cannot accomplish.

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* Recherches Expérimentales sur les Propriétés et les Fonctions du Système Nerveux. Paris, 1842, pp. 37, 53, 102, 133.

The inference from these phenomena is that the power of coördination for voluntary movements resides in the cerebellum, and is impaired by injury of its substance. We have already seen (page 407) that, for the body and limbs, in the acts of standing and locomotion, a power of coördination exists in the spinal cord; and that it apparently depends on the integrity of the posterior columns, which serve as connecting longitudinal tracts between its different parts. But to produce an appreciable disturbance of this power in the spinal cord, the posterior columns must be divided at several successive points; thus disassociating its parts from each other for a considerable extent. The cerebellum is the only nervous centre in which a single injury produces a want of coördination for all voluntary movements whatever. According to this view, it is a nervous centre of highly developed structure, superadded to the cerebro-spinal tracts, for the complicated association of their motor impulses. This association cannot be properly carried out in any particular part, unless the corresponding peripheral tracts be also in a state of integrity; but it is in the gray substance of the cerebellum that the nervous coördination is originally effected.

Restoration of the Coördinating Power in Operated Animals.—It is a remarkable fact that after the coördinating power has been seriously impaired by partial destruction of the cerebellum, it may in some instances be recovered, without regeneration of the nervous substance. This recovery was observed by Flourens both in the fowl and in the pigeon, and has been seen by Flint* in the pigeon after removal of about two-thirds of the cerebellum. We have also met with four instances of the same kind. In the first, about two-thirds of the cerebellum were taken away by an opening in the posterior part of the cranium. Immediately afterward, the pigeon showed all the usual effects of the operation, being incapable of flying, walking, or even of standing still, but only reeled and sprawled in a perfectly helpless manner. In five or six days he had regained a considerable control over the voluntary movements, and at the end of sixteen days his power of muscular coördination was so nearly perfect that its deficiency, if

FIG. 117.

BRAIN OF HEALTHY PIGEON—Profile view.—1. Cerebral Hemisphere. 2. Optic Tubercle. 3. Cerebellum. 4. Optic Nerve. 5. Medulla Oblongata.

FIG. 118.

BRAIN OF OPERATED PIGEON—Profile view—showing the mutilation of the Cerebellum.

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* The Physiology of Man; Nervous System. New York, 1872, p. 367.

any existed, was imperceptible. He was then killed, and on examination it was found that his cerebellum remained in nearly the same condition as immediately after the operation; about two-thirds of its substance being deficient, with no regeneration of the lost parts. The accompanying figures show the appearances in this brain as compared with that of a healthy pigeon.

In the three remaining cases the quantity of nervous substance removed amounted to about one-half of the cerebellum. The loss of coördinating power, immediately after the operation, though less complete than in the preceding instance, was perfectly well marked; and in little more than a fortnight the animals had nearly or quite recovered control of their motions, so far as could be seen while they were under observation.

It is evident that in these cases, if the cerebellum be really the physiological seat of coördinating power, there are two distinct effects produced by the operation. The first is the shock due to the *sudden injury of the cerebellum as a whole.* This effect is temporary, and may be recovered from in time, provided the animal survive the immediate injury. The remaining effect is that due to *the loss of nervous substance;* and this effect must of course be permanent, unless the nervous matter be regenerated. In the cases detailed above, the greatest amount of disturbance seems to have depended on the sudden injury to the nervous centre as a whole; and the animals recovered, to a great extent, their power of coördination, notwithstanding that from one-half to two-thirds of the cerebellum was permanently lost.

The recovery of a nervous function, after loss of substance, is not peculiar to the cerebellum. Flourens observed the same thing in regard to the cerebral hemispheres in the pigeon: the perceptive faculties being totally suspended by removal of a portion of the hemispheres, and again restored after several days. But this restoration only takes place where the removal of the nervous centre is partial; and in the cerebellum, as well as in the cerebrum, after complete extirpation, the loss of function is permanent. In the experiment of Flourens, where a fowl lived for four months after entire removal of the cerebellum, there was no recovery of coördinating power.

The recovery of this power after partial loss of the cerebellum may be also in some measure apparent rather than real. The animals may, after a time, cease attempting the more complicated movements of which they are incapable, and confine themselves to the simpler acts which they can still accomplish. A pigeon, furthermore, when confined to the limited space of a laboratory, has no opportunity for the many varied evolutions of natural flight; and it is possible that he might be permanently incapacitated for such movements, while showing no deficiency in the ordinary acts of standing or progression.

The same remark will apply to certain pathological observations in man, which have been sometimes considered as neutralizing the results of experiment on this subject. These are mainly cases in which lesions of the cerebellum, more or less extensive, have existed without recorded disturbances of muscular coördination. A large majority of these patients were confined to a sick-room, and many of them to the bed; consequently there could be no opportunity of observing a want of natural coördination in the more complicated movements, if any such existed. A patient, suffering from the gradual diminution of a nervous function, accommodates himself to it by abstaining from the attempt to do what he knows is impossible, and endeavors to accomplish his objects by other means. Moreover, in many cases of disease of the cerebellum, symptoms of want of coördinating power have been distinctly recorded.

The data derived from *comparative anatomy* show a general correspondence in the development of the cerebellum and the variety of muscular action. In fish, as a rule, it is of good size compared with other parts of the brain; and although direct progression in this class is accomplished by a comparatively simple mechanism, namely, the lateral flexion and extension of the spinal column with its expanded fins and tail, yet their movements through the water or in leaping out of it, while pursuing and taking their prey, are rapid and vigorous, and are promptly varied in any direction. In the frog, on the other hand, the movements of progression consist of little else than straightforward flexion and extension of the posterior limbs; and the cerebellum is much inferior in size to that of fishes, forming only a thin narrow ribbon of nervous matter across the upper part of the fourth ventricle. In turtles, locomotion is accomplished by consentaneous action of the anterior and posterior limbs, while the cerebellum exhibits a corresponding increase of development. In the alligator, whose motions approximate still more closely to those of the quadrupeds, the cerebellum is also larger in proportion to the remaining parts of the brain. In birds, in quadrupeds, and in man there is a very evident increase in the size and convolutions of the cerebellum, corresponding with the greater variety and delicacy of their movements. These facts are not decisive in determining the physiological function of this portion of the brain; but they show that the assumption of a coördinating power in the cerebellum is not at variance with its comparative anatomy.

All that we know with certainty, therefore, in regard to the cerebellum, indicates its close connection with the power of coördination. By its inferior peduncles it is in communication with the posterior columns of the spinal cord, and by its superior peduncles with the upper portion of the crura cerebri; and, so far as its function can be demonstrated from experiment, it appears to act as a general centre of combination for voluntary movement.

The Medulla Oblongata.

The medulla oblongata is distinguished from the spinal cord, of which it forms the direct continuation, by its expanded form, the different appearance of its longitudinal tracts, and especially by the changed position and special properties of its gray substance.

The arrangement of the gray substance is one of the most characteristic features of the medulla oblongata. First, it increases in quantity from below upward; and, secondly, it undergoes a complete alteration in form and position. In the spinal cord it presents the well-known figure, on transverse section, of a central mass extending on each side into the anterior and posterior horns. But in the medulla oblongata it recedes into a backward position; its posterior horns spreading out laterally, and the remainder occupying the space between them. The posterior median fissure also becomes shallower and wider by the divergence of the posterior columns; and the central canal approximates the posterior wall of the medulla, finally opening upon its surface at the lower part of the fourth ventricle. The gray substance of the medulla is thus uncovered posteriorly, forming a superficial layer on each side the median line, immediately beneath the floor of the fourth ventricle. It thence extends forward, without complete interruption, through the whole length of the fourth ventricle and about the aqueduct of Sylvius; giving origin, at various points in this situation, to the root-fibres of all the cranial nerves, excepting the olfactory and the optic.

Physiological Properties of the Medulla Oblongata.—The physiological properties of the medulla are more distinctly marked than those of any other part of the encephalic mass. It is in a high degree both sensitive and excitable, especially in its posterior portions. Either mechanical or galvanic irritation gives rise at once to signs of sensation, if the rest of the brain be uninjured, and in the recently killed animal produces convulsive movements of considerable intensity. These effects are due to irritation of the longitudinal fibres connecting the medulla with the spinal cord, and of the sensitive and motor cranial nerve roots. Since the medulla is the only bond of nervous communication between the brain and the spinal cord, its section at any point also destroys voluntary motion and sensibility in the body and limbs.

Action of the Medulla Oblongata as a Nervous Centre.—The various deposits of gray substance in the medulla, and their connection with nerves of widely different distribution and functions, are the peculiar features of its anatomical structure; while its reflex actions are also of a special and distinctive character.

The most important action of the medulla as a nervous centre is that connected with *respiration*. So long as the medulla is uninjured, although the cranium be emptied of all its other nervous centres, respiration goes on without essential modification. But if the other parts of the brain be left intact and the medulla be destroyed, in any warm-blooded animal, all movements of respiration cease instantaneously. The circulation still continues for a time; but as the blood becomes deficient in aeration, it is gradually retarded and after several minutes comes to an end. The effect of this operation upon the two functions of circulation and respiration is very different. The circulation is interfered with and finally arrested as a secondary consequence, because the blood is no longer arterialized; but respiration is abolished at once, as an immediate result of injury to the medulla.

As the movements of respiration are performed by the consentaneous action of different muscles, the effect of an injury to the cerebro-spinal axis will vary according to its locality. The respiratory movements of the chest and abdomen are arrested by section of the cord anywhere above the third cervical vertebra, since this paralyzes both the diaphragm and the intercostal muscles. But movements of inspiration, simultaneous with those of the chest and abdomen, are also performed by the glottis; and in most quadrupeds there is at the same time an expansion of the nostrils, all associated with each other in the act of respiration. If the spinal cord be divided at the third cervical vertebra the movements of the chest and abdomen cease, but those of the glottis and nostrils continue, since the nerves supplying these parts are still in communication with the medulla oblongata. But destruction of the medulla arrests at the same instant all movements of respiration, both in the trunk, the glottis, and the face.

The medulla accordingly is a centre from which the whole respiratory apparatus derives its stimulus, and in man, quadrupeds, and birds it is the most important part of the brain for the immediate preservation of life.

The more exact location of the respiratory centre was investigated by Flourens[*] by making transverse sections of the medulla at different parts of its length, and observing the effect produced. The result showed that such injuries, inflicted just behind the point of emergence of the pneumogastric nerves, destroyed all the movements of respiration together. Below this point, the movements of the chest and abdomen were stopped, but those of the nostrils and glottis continued; above it, the movements of the nostrils were arrested, while those of the chest and abdomen went on.

Flourens subsequently[†] limited the position of this centre still more closely. In rabbits it occupies a space of about 2.5 millimetres on each side the median line, situated at the lower end of the fourth ventricle, a little in advance of the divergence of the posterior pyramids, and just at the point of gray substance formed by the *ala cinerea*. A section of the medulla at this spot, with a double-edged knife only 5 millimetres wide, or its perforation at the same point with a sharp-edged canula not more than 3 millimetres in diameter, caused immediate stoppage of respiration; while this effect was not produced by similar injuries either above or below. This spot, which contains the nervous centre of respiration, corresponds, in man, on the front of the medulla oblongata, with the upper end of the decussation of the ante-

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[*] Recherches Expérimentales sur les Propriétés et les Fonctions du Système Nerveux. Paris, 1842, pp. 196–204.

[†] Comptes Rendus de l'Académie des Sciences. Paris, 1858, tome xlvii., p. 803.

rior pyramids, or the lower extremity of the olivary bodies, and is somewhat below the apparent origin of the pneumogastric nerves.

Respiration accordingly is an act consisting of various associated movements, which have their nervous centre in the medulla oblongata. The movements themselves are involuntary in character; for although those of the chest and abdomen may be for a short time increased in frequency, the surplus movements thus performed are not necessary to respiration, and soon produce a fatigue which prevents their continuance. Respiration goes on with its natural rhythm, unaccompanied by fatigue, under the influence of the medulla, from the moment of birth, without necessary consciousness of its existence. If arrested by voluntary effort, the internal stimulus which prompts it grows gradually more urgent, until the will can no longer withstand its demands; and as soon as voluntary resistance is discontinued, the movement recommences under the independent action of the medulla oblongata.

The function of the medulla in respiration is usually regarded as a reflex act. According to this view, its gray substance is sensitive to a stimulus derived from the lungs and other vascular organs, which gives notice of a commencing deficiency in respiration. This excites in the medulla a motor impulse, which is reflected in the centrifugal direction and calls into activity the respiratory muscles. In normal respiration the reflex action of the medulla takes place without an appreciable sensation. On the renewal of air in the lungs by inspiration, the unconscious demand is satisfied, the muscles relax, and expiration follows by passive collapse of the lungs and thorax. In a few seconds, as the oxygen is consumed and carbonic acid accumulates, the previous condition recurs and the action is repeated as before, thus causing the rhythmical alternating movements of inspiration and expiration.

The evidence that the medulla acts in this way as a reflex centre for respiration is mainly of two kinds. First, the sudden contact of an external stimulus, such as a dash of cold water on the skin, or the application of a pungent vapor to the nostrils, causes almost invariably an involuntary inspiration. As the medulla is the sole nervous centre for respiratory movements, the external impression in these cases must be conveyed by centripetal fibres to its gray substance, exciting there the special motor stimulus of respiration. Secondly, division of the pneumogastric nerve, an operation which shuts off from the medulla all influences derived from the lungs, causes immediate diminution in the frequency of respiration; a result which may be explained by supposing that the most effective stimulus to the medulla as a respiratory centre is received from the lungs through this nerve.

A different view of the action of the medulla in respiration is taken by Foster * and by Flint.† According to these writers, the medulla

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* Text-book of Physiology. London, 1879, p. 334.

† American Journal of the Medical Sciences. Philadelphia, 1880, vol. lxxx., p. 69.

generates within itself the nervous stimulus to respiration, independently of external impressions. The immediate cause of its action is attributed by Flint to a deficiency of oxygenated blood in its capillary vessels, by which it is excited to momentary activity. The author sustains this view by the result of experiments on animals, in which involuntary movements of respiration were excited by cutting off the supply of arterial blood from the medulla and other parts of the encephalon. But both these authors agree in considering the medulla as in some way the indispensable nervous centre for respiration.

An irregularity in the movements of respiration is, accordingly, one of the most threatening symptoms in affections of the brain. Cerebral apoplexy at the surface of the hemispheres, in the lateral ventricles, or in the cerebral ganglia, is seldom immediately fatal, however extensive the injury. But when occurring in the medulla oblongata or its immediate neighborhood, it produces death instantaneously by the same mechanism as where this part is destroyed by experiment in animals. When the medulla is implicated, in man, by progressive disease or by failure of its nervous functions, the respiratory movements first affected are those of the face, while those of the chest and abdomen go on for a time as usual. The cheeks are drawn in with every inspiration and puffed out with every expiration, the nostrils sometimes participating in these abnormal movements. A still more dangerous symptom, which frequently precedes death, is an irregular and hesitating respiration, usually noticeable after the remaining cerebral functions have been already impaired. These phenomena depend on the connection between respiration and the medulla as a nervous centre.

Deglutition is also under the control of the medulla. Mastication of the food, and its transfer by the tongue to the entrance of the fauces, are voluntary actions, which may be continued or arrested at will. But when the food has passed from the mouth into the pharynx, the process of deglutition, by which it is carried down into the stomach, is reflex and involuntary. Once commenced, it cannot be arrested by the will, as it consists of muscular contractions following each other in undeviating succession, and receiving their impulse from the medulla oblongata. In the experiments of Flourens and Longet, fowls and pigeons, after removal of the cerebral hemispheres, never picked up their food spontaneously, nor even swallowed it when placed in the mouth at the end of the beak; but if carried backward into the pharynx, it was at once embraced by the muscular walls of this organ, and carried into the stomach by a continuous movement of deglutition. This movement includes, not only the associated contraction of the pharynx and œsophagus, but also the stoppage of respiration and closure of the glottis, by which the food is prevented from passing into the larynx. According to Vulpian, after all parts of the brain have been removed, in cats or guinea-pigs, excepting the medulla, swallowing may still be accomplished by reflex action; but it becomes impossible as soon as this part is removed or seriously injured. The necessary muscular combinations cannot take place, except under the influence of the medulla as a nervous centre.

Deglutition may consequently be performed, in man, after conscious sensibility and voluntary power have disappeared. In compression of the brain from injury or disease, when the individual is completely unconscious, and even when respiration has become diminished in frequency, solid or liquid food, if carried into the upper part of the pharynx, may be successfully swallowed by the ordinary movements. When this process is no longer possible, or is accompanied by choking or regurgitation, it indicates that the medulla has become seriously affected, and that death is probably near at hand.

The medulla is furthermore connected with *phonation.* A vocal sound is usually caused by a voluntary impulse from the cerebral hemispheres. It may also be a purely emotional act, without any reasonable or intelligent motive. But in both cases its actual production is a secondary result, requiring special nervous combinations, the immediate centre of which is located in the medulla. This is shown by the fact that a cry may still be produced, under an irritation applied to the medulla, when the upper parts of the encephalon have been removed. If a stilet be introduced into the cranium of a frog, the cerebral hemispheres may be broken up without producing any excitement of the vocal organs; but the contact of the instrument with the medulla is often followed by a spasmodic cry. Vulpian has shown that a similar effect may be produced in mammalians by reflex action, after removal of the whole encephalon excepting the medulla; a cry being produced each time the foot is pinched by a forceps. This sound, however, gives no indication of consciousness or sensibility on the part of the animal. It is short, abrupt, and momentary, and is repeated only when the irritation is again applied to the external parts. After destruction of the medulla, on the other hand, no vocal sound can be produced, and irritation of the integument is followed only by the ordinary movement of the limbs, dependent on reflex action of the spinal cord.

In the exercise of the voice, therefore, the preliminary actions of intelligence, volition, or emotional excitement require the coöperation of other parts of the encephalon; but the immediate mechanism by which a vocal sound is produced has its nervous centre in the medulla oblongata.

The medulla oblongata, with the adjoining part of the tuber annulare, is also the direct source of the movements of *articulation.* It is the gray substance of this region that gives origin to the hypoglossal and facial nerves distributed to the muscles of the tongue and lips, and to the motor fibres of the pneumogastric nerve, which regulate the condition of the rima glottidis. Disease or injury in this situation, sufficient to impair nervous action, consequently makes articulation difficult or impossible. This affection is quite distinct from "aphasia," which is of cerebral origin, and in which the external mechanism of speech is unaffected, the muscles of the tongue and lips retaining their normal power of movement. In disease of the medulla, on the other hand, the muscular paralysis is very evident, and is mainly confined to the muscles of articulation and phonation.

Such a disease is that known as *glosso-labio-laryngeal paralysis.* It is a paralysis due to chronic degeneration of the gray substance in the medulla oblongata, and affects the motor nerves of the tongue, the face, the hanging palate, and the larynx. The first difficulty is generally noticeable in the movements of the tongue, which cannot be applied accurately to the teeth or the roof of the mouth; the lingual and dental consonants being therefore pronounced imperfectly or not at all. The lips are next affected, so that they cannot be brought in contact with each other, and B and P are pronounced like V or F. As the debility of the orbicularis oris increases, entirely preventing approximation of the lips, the vowels O and U are no longer sounded; and, by the continued exaggeration of these difficulties, the patient's speech becomes at last unintelligible. Deglutition is also affected, and the attempt to swallow is liable to cause choking from imperfect protection of the rima glottidis. Phonation becomes impaired from debility of the laryngeal muscles, and in advanced cases no vocal sound can be produced. The disease is uniformly progressive, and usually terminates by affecting the movements of respiration.

The medulla oblongata is, accordingly, the seat of reflex actions connected with the immediate preservation of life, since it maintains the movements by which air and food are introduced into the body. It also presides over the muscular combinations concerned in the voice and articulation, and by this means establishes an intelligible communication with the external world.

CHAPTER VI.

THE CRANIAL NERVES.

THE cranial nerves, which take their origin from the base of the brain, are in great measure analogous in anatomical and physiological character, with the spinal nerves. An exception to this rule exists only in the three nerves of special sense, the olfactory, optic, and auditory, which are endowed neither with tactile sensibility nor motor power, and which are connected in a special way with the gray substance of the hemispheres.

The remaining cranial nerves are distributed either to the integument, mucous membranes, or muscular tissues, and are either sensitive or motor, or have both properties combined. Some of them, like the oculomotorius, the patheticus, and the facial, are distinctively motor in character, are distributed to muscles, produce convulsive motion on being irritated, and, when injured or divided, leave the corresponding parts in a state of paralysis. Others, such as the trigeminus, the glosso-pharyngeal, and the pneumogastric, are sensitive nerves, possessing either an acute tactile sensibility, like the trigeminus, or one of more special nature, like the glosso-pharyngeal and pneumogastric. Like the posterior roots of the spinal nerves, they are provided with a ganglion near their points of emergence from the base of the brain; and they are distributed either to the integument or mucous membranes or to both.

The anatomical similarity between the cranial and spinal nerves is in some instances very marked. The fifth pair, or trigeminus, emerges from the tuber annulare by two roots, of which one is sensitive, the other motor; the sensitive root presenting a well developed ganglion, with which the fibres of the motor root do not mingle. Beyond the ganglion, accordingly, the nerve contains both motor and sensitive fibres, and is distributed both to muscles and to the integument. The glosso-pharyngeal nerve is joined, beyond its ganglion, by motor fibres from the facial; and the pneumogastric receives communications from the spinal accessory and other motor nerves. Both sensibility and motion are therefore provided for, in a manner not essentially different, by the cranial and spinal nerves.

The other points, both of difference and analogy, in the cranial nerves, relate to their origin and distribution. Their apparent origin, or the point at which they become detached from the surface of the brain, is not their real origin; but in every case their fibres can be traced inward, often for a considerable distance, between the tracts of white substance, until they reach a central mass of gray matter from which they originate, and which is called their "nucleus." For all except the olfactory and optic nerves, these nuclei of origin are situated along the floor of the fourth ventricle or about the aqueduct of Sylvius.

The peculiarities of peripheral distribution, in the cranial nerves, are more apparent than real in importance. The oculomotorius, patheticus, and abducens emerge from the brain at very different points, and, running forward through the cranial cavity in the form of separate cords, are enumerated as three nerves. But they all originate from the same layer of gray substance, two of them, the oculomotorius and the patheticus, in close proximity to each other; they all pass from the cranial into the orbital cavity by the sphenoidal fissure; and they are all distributed to muscles moving the eyeball. In a physiological point of view, therefore, they are branches of a single nerve. Even when two or more nerves emerge from the cranium by different foramina, like the three divisions of the trigeminus, they are nevertheless, properly speaking, parts of the same nerve, if they have similar physiological properties and are distributed to the same region. It is the character and ultimate destination of a nerve, and not its course through the bones of the skull, which determine its physiological position. In the bull-frog, as shown by Wyman,* both the facial nerve and the abducens are given off as branches from the fifth pair; and in most quadrupeds, the frontal branches of the ophthalmic division of the trigeminus are nearly wanting, in accordance with the imperfect sensibility of the forehead and vertex.

The cranial nerves may, therefore, be conveniently arranged in pairs according to their distribution and functions, notwithstanding the incidental peculiarities of their course or subdivision. The olfactory, optic, and auditory nerves form a separate specific group; while the remainder consist of motor and sensitive nerves, supplying the muscles and integument of different regions.

Cranial Nerves.

Nerves of Special Sense.

1. Olfactory. 2. Optic. 3. Auditory.

	Motor nerves.	Sensitive nerves.	Distributed to the
1st PAIR.	Oculomotorius Patheticus Abducens Facial Small root of 5th pair	Trigeminus.	Upper, middle, and lower facial regions.
2d PAIR.	Hypoglossal	Glosso-pharyngeal.	Tongue and pharynx.
3d PAIR.	Spinal accessory	Pneumogastric.	Passages of respiration and deglutition.

This division of the cranial nerves, according to their physiological character, is not perfect in all particulars. For while the hypoglossal

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* Nervous Systems of Rana pipiens. Smithsonian Institution; Washington, 1853.

nerve supplies only the muscles of the tongue, its associate, the glosso-pharyngeal, sends part of its sensitive fibres to the tongue and part to the pharynx; and while the trigeminal nerve is mainly distributed to the external parts of the face, one of its deeper branches, the lingual, is distributed to the tongue. The arrangement, however, is substantially correct, and may serve as a useful guide in the study of the nervous functions.

First Pair. The Olfactory Nerves.

What is called in man the "olfactory nerve," is a prismatic extension of gray and white substance, running in a longitudinal groove on the under surface of the anterior cerebral lobe, near the median line, and terminating anteriorly in a flattened ovoid mass of gray substance, the "olfactory bulb." The olfactory bulb rests upon the cribriform plate of the ethmoid bone, and gives off, through the perforations in this bone, the nervous filaments supplying the olfactory membrane in the nasal passages. The prismatic mass connecting the olfactory bulb with the rest of the brain is, in reality, an extension of the anterior lobe, and forms part of the cerebral convolutions. In most quadrupeds it is much larger than in man, often enclosing a prolongation of the lateral ventricle; and in size and structure it exhibits so close a resemblance with the remaining convoluted portion of the brain, that it is properly designated as the "olfactory lobe." In man it is so slightly developed that this term can hardly be applied to it; but it nevertheless consists partly of gray substance, and shows only on its superficial border a longitudinal striation of white substance, which connects the olfactory bulb in front with the central parts of the brain behind.

The olfactory apparatus consists accordingly of, 1st, the olfactory *nerves* proper, distributed upon the mucous membrane of the upper part of the nasal passages, and connected at their central extremity with the gray substance of the olfactory bulb; 2d, the olfactory *bulbs*, situated on the anterior extremity of the olfactory lobes, and giving origin, as above described, to the nerves of the olfactory membrane; and 3d, the olfactory *tracts*, that is the longitudinal bands of white substance, running along the superficial border of the olfactory lobes (commonly called "olfactory nerves"), toward the central parts at the base of the brain.

Physiological Properties of the Olfactory Nerve.—The connection of the olfactory nerve with the sense of smell is indicated by, 1st, its anatomical relations; 2d, its comparative development in different animals; and 3d, the results of its injury or disease.

I. The only anatomical connection of the olfactory tracts, at their anterior extremity, is with the olfactory bulb; and the nerve fibres given off from this part are distributed only to the olfactory region of the nasal passages. In this region ordinary sensibility is but slightly developed, while it is highly endowed with the sense of smell.

II. In animals possessing a more acute sense of smell than man, like the dog, cat, sheep, and most other quadrupeds, both the olfactory bulbs and the olfactory tracts are increased in a similar ratio. There is accordingly a direct correspondence between their development and that of the special sense with which they are connected.

III. A number of cases are quoted by Longet in which congenital absence of the olfactory nerves, in man, was accompanied by congenital incapacity to distinguish odors; and others in which loss of smell was observed after affections causing their compression or destruction.

Finally, experimental division or destruction of these nerves in dogs abolishes, so far as observation can show, the power of discriminating odors; although it leaves the nasal mucous membrane sensitive to pungent or caustic vapors. In the experiments of Magendie,* a dog, after destruction of both olfactory nerves, would disentangle a package containing meat when openly presented to him; but he did not find it, when placed near by without his knowledge. The same result was obtained by Vulpian† in experiments upon hunting dogs. These animals, after recovering from the immediate effects of the operation, were kept fasting for two days, and then introduced into an apartment where a piece of cooked meat was concealed; but they were never able to discover it, when the division of the nerves had been complete. Notwithstanding, therefore, the difficulty of experimenting upon so obscure a function as that of smell, there is no doubt that the olfactory nerves and bulbs are the internal organs of the olfactory sense, and that they are disconnected both with ordinary sensibility and the power of motion.

Second Pair. The Optic Nerves.

The optic nerves are distinguished by their very prominent decussation at the base of the brain, where they present the appearance of being consolidated with each other. By this decussation, which is called the "chiasma,"‡ they are divided into two portions. The optic nerves proper, situated in front of the chiasma, are nearly cylindrical in form and consist of fibres coming directly from the retina on each side. Behind the chiasma they are known as the "optic tracts," and appear as flattened bands of nerve fibres, connecting the visual organs with the central parts of the brain. The optic tract on each side, after following the contour of the crus cerebri in a backward direction, divides into two roots, an internal and an external. The internal root is connected with the corpus geniculatum internum, through and over which its fibres pass, continuing their course upward and backward until they reach the anterior tubercula quadrigemina. The external root, which is the larger of the two, is attached to the corpus geniculatum externum.

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* Journal de Physiologie Expérimentale et Pathologique. Paris, 1825, tome iv., p. 170.

† Leçons sur la Physiologie du Système Nerveux. Paris, 1866, p. 882.

‡ This term is of Greek origin, and is derived from a verb which signifies to mark with the letter χ.

Here some of its fibres are connected with the gray substance of this ganglion; while others pass onward to their termination in the posterior part of the optic thalamus. This represents the central connection of the optic tracts, as described by Wagner, Henle, and Huguenin, and as generally accepted by modern anatomists. The optic tracts have accordingly their origin in three separate nuclei or deposits of gray substance, namely, 1st, the anterior tubercula quadrigemina; 2d, the corpus geniculatum externum; and 3d, the optic thalamus.

But there are, beyond question, further indirect connections between these nuclei and the cortex of the hemispheres. They consist of diverging fibres from both the optic thalamus and the corpora geniculata, which, according to Gratiolet, Meynert, and Huguenin,* take part in the formation of the corona radiata and pursue their course toward the posterior part of the hemispheres.

Physiological Properties of the Optic Nerves.—The optic nerves are nerves of special sense, and may be regarded as tracts of fibres connecting the gray matter of the cerebrum with the retinal expansion in the eyeball. They are destitute of tactile sensibility and convey inward only the impression caused by luminous rays. In the central parts of the brain this impression produces the sensation of light; and the optic nerves are therefore the channels for the sense of vision. Magendie found in quadrupeds both the retina and the optic nerves throughout their length insensible to mechanical irritation; and, in man, touching the retina with a cataract needle excited no perceptible sensation. It has also been remarked, in cases of extirpation of the eyeball, that section of the optic nerve is not painful; and, according to Longet, these nerves in the lower animals may be pinched, pricked, cauterized, divided, or injured in various ways without causing signs of pain.

On the other hand, their division at once produces blindness. The impressions received by the retina are no longer transmitted to the central organ, and the animal becomes insensible to light, without any loss of tactile sensibility or the power of motion.

Beside their immediate function in the perception of light, the optic nerves are the channels for a special reflex action; namely, that of the *contractile movements of the iris.*

These movements, by which the quantity of light admitted to the eye is regulated by the size of the pupil, are involuntary in character, but are due to impressions conveyed inward by the optic nerve. The impression, first received upon the retina, passes through the optic nerve to the tubercula quadrigemina. Its transformation into a motor impulse is either accomplished in these bodies, or is commenced in them and completed by transmission to the nucleus of origin of the oculomotorius nerves. Thus both the optic nerves and the tubercula quadrigemina are essential to the movements of the pupil under the influence of light.

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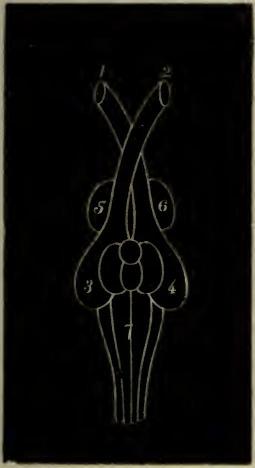
* Anatomie des Centres Nerveux. Paris, 1879, pp. 111, 135.

That this is a reflex action is shown by dividing and irritating the optic nerves. After section of the nerve, according to the experiments of Mayo and Longet, upon pigeons, dogs, and rabbits, irritation of its *peripheral* end, that is, the portion still connected with the eyeball, produces no effect on the pupil; but irritation of its *central* portion, which is connected with the brain, at once causes contraction. On the other hand, division of the oculomotorius nerve paralyzes the iris and puts an end to the movements of the pupil, although the eye may be otherwise uninjured and the perception of light unimpaired.

Decussation of the Optic Nerves.—The decussation of the optic nerves, which in man and all vertebrate animals is visible on superficial examination, varies considerably in its details in different classes. These variations may be mainly referred to three distinct types, generally known to comparative anatomists, and more distinctly recognized in the recent investigations of Nicati.*

FIG. 119.



INFERIOR SURFACE OF THE BRAIN OF THE COD.—1. Optic nerve of right eye. 2. Optic nerve of left eye. 3. Right optic tubercle. 4. Left optic tubercle. 5, 6. Cerebral hemispheres. 7. Medulla oblongata.

FIG. 120.

INFERIOR SURFACE OF THE BRAIN OF FOWL.—1. Optic nerve of right eye. 2. Optic nerve of left eye. 3. Right optic tubercle. 4. Left optic tubercle. 5, 6. Cerebral hemispheres. 7. Medulla oblongata.

I. In fishes and reptiles the optic nerves cross each other without commingling, so that their complete decussation is visible to the unaided eye. In many instances, as in the cod (Fig. 119), each nerve, preserving its cylindrical form, passes either above or below its fellow to the eye of the opposite side. In others, as in the herring, the nerve of the right side passes through a slit or fenestra in that of the left; and in others still, the decussation takes place by several distinct bundles of fibres crossing at various levels above or below each other. Throughout these two classes it is plainly evident that all the optic fibres com-

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* Archives de Physiologie. Paris, 1878, 2^{me} sèrie, tome v., p. 658.

ing from one side of the brain go to the eye of the opposite side, and *vice versa.*

II. In birds the optic nerves appear superficially to be united at the chiasma, but dissection shows that they are only broken up into fasciculi of fibres which, though interwoven with each other, remain anatomically distinct (Fig. 120). The fasciculi of each nerve, generally eight in number, cross the median line at the point of decussation, so that the retina of each eye is exclusively supplied with nerve fibres from the opposite side of the brain. Experiment furthermore shows that in the pigeon, removal of the optic tubercle on one side produces complete blindness in the opposite eye.

III. In the mammalia, and in man, the two optic nerves are so intimately consolidated at the chiasma, that the course of their respective fibres cannot be determined by simple inspection, nor by the ordinary means of dissection, but requires the aid of hardening fluids and microscopic sections. These methods demonstrate that in all cases there is a decussation at the median line. According to Henle, the decussating fibres, in man, are arranged in laminæ, about $\frac{1}{50}$ of a millimetre in thickness, which cross above and below each other from side to side; while in front and behind the chiasma sections of the optic nerves and tracts present only the appearance of longitudinal fibres. All anatomists are agreed that the greater part of the optic fibres decussate in this way at the chiasma. But the majority also admit that this decussation, in man and most quadrupeds, is incomplete; a portion of the fibres of each tract, situated upon its outer border, passing to the eye of the same side, while the remainder cross at the chiasma, to the eye of the opposite side. Each eye is supplied, according to this view, with nerve fibres from the opposite optic tract and opposite side of the brain, and also with fibres from the optic tract and the brain on its own side. There is, furthermore, a transverse band of fibres, admitted by all modern writers, passing across, at the posterior border of the chiasma, from one optic tract to the other. This band is the only part of the chiasma which remains intact after destruction of both eyeballs and consequent atrophy of the optic nerves and tracts. It is considered as a transverse commissure between corresponding parts of the brain, and as having no direct connection with the sense of vision. The partial decussation of the optic nerve, in man and the higher quadrupeds, is regarded by many, and especially by Henle,* as demonstrated on anatomical grounds. The possibility of this is denied by others; and the existence of direct fibres, in addition to those which decussate, is no doubt largely inferred from the partial disturbance of vision in pathological cases, and from the results of physiological experiment. In birds, as above stated, the complete decussation of the optic nerves at the chiasma is demonstrable by dissection; and removal of one optic tubercle causes absolute blindness on the opposite side without perceptible loss of sight

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* Handbuch der Nervenlehre des Menschen. Braunschweig, 1879, p. 389.

on the same side. If the decussation were also complete in quadrupeds, a longitudinal section of the chiasma at the median line would divide at once all the optic nerve fibres, and produce blindness of both eyes. But Nicati* has shown, by experiments on cats, that after such a section vision still exists in these animals in an unmistakable degree; showing that the eyes receive through the optic nerves some fibres which have not crossed the median line. From a comparison of the form and section surfaces of the optic tracts and chiasma, he finds that the same conclusion is applicable to man.

FIG. 121.

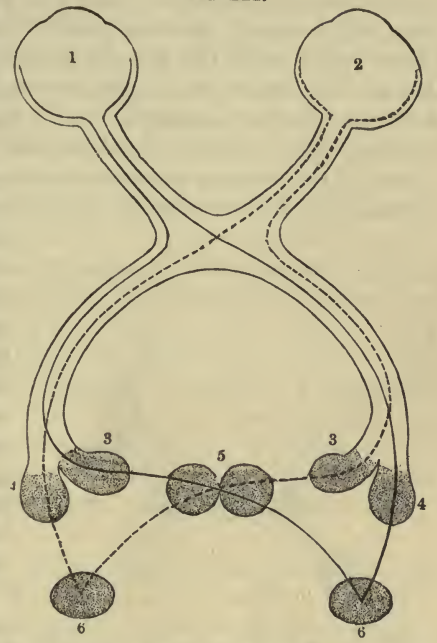

DIAGRAM OF THE OPTIC NERVES AND TRACTS, in Man.—1. Left eyeball. 2. Right eyeball. 3, 3. Corpora geniculata interna. 4, 4. Corpora geniculata externa. 5. Tubercula quadrigemina. 6, 6. Centres of vision in the cerebral hemispheres.

Disturbances of Vision from Lesion of the Optic Nerves or Tracts.—There are certain varieties of partial or complete blindness in one or both eyes, occurring in man, which are only explainable on the supposition of incomplete decussation of the optic nerves. They depend on lesion or compression of the optic fibres at different parts of their course. Complete *blindness of one eye* is produced by a lesion involving the whole of one optic nerve, between the chiasma and the eyeball, as at A, Fig. 122; since such an injury interrupts all the nerve fibres, from whatever source, going to the retina of the corresponding eye.

In the affection known as *hemiopia,* the patient sees only one lateral half of objects presented to his view. His field of vision, instead of being circular, has the form of a semicircle; being divided at its middle by a vertical diameter, on one side of which everything is invisible. Such a condition may be produced by lesions affecting one of the optic tracts behind the chiasma, as at B, Fig. 122. As the direct fibres, on the outer border of each tract, pass to the external portion of the retina on the same side, and the cross fibres pass to the internal portion of the opposite eye, both eyes will be blinded in the corresponding half of the retina, and for the opposite half of the field of vision. If the lesion involve the left optic tract, as in Fig. 122, the right lateral half of the

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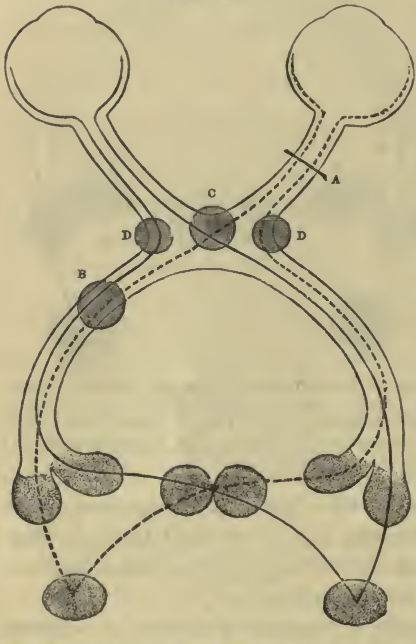
* Archives de Physiologie. Paris, 1878, 2me série, tome v., p. 658.

field of vision will be obliterated; since it is the left half of each retina which receives rays coming from the right side, and *vice versâ.*

On the other hand a lesion situated at the front of the chiasma, and on the median line, as at C, Fig. 122, will interrupt only the crossed fibres, which supply the inner portion of both eyes. This will produce a hemiopia in which the left eye is blind for the left half of the visual field, and the right eye is blind for its right half. The whole field of vision is therefore perceptible when both eyes are used; but when either of them is covered, the defect becomes apparent.

Exactly the opposite condition is that in which the left half of the field of vision is obliterated for the right eye, and the right half for the left eye. This may be caused by injuries affecting simultaneously the outer border of the chiasma on both sides, as at D, D, Fig. 122; by which the direct fibres going to each eye are interrupted, while the cross fibres remain intact. According to the citations of Charcot,* all these forms of hemiopia have been observed in company with the corresponding lesions.

Fig. 122.



Lesions of the Optic Nerves and Tracts.—A. Lesion of Right Optic Nerve; blindness of Right Eye. B. Lesion of Left Optic Tract; hemiopia of left side, both eyes. C. Lesion of Decussating Fibres of the Chiasma; internal hemiopia, both eyes. D, D. Double Lesion of Direct Fibres; external hemiopia, both eyes.

Lastly, *unilateral blindness,* that is, blindness of one eye (amblyopia), may be produced by cerebral lesions, independently of any injury to the optic nerves or tracts. It has already been seen (page 430) that in the dog unilateral blindness, on the opposite side, may result from destruction of a portion of the cortical layer of the hemisphere. In man, as shown by Charcot,† hemianæsthesia, from lesion of the posterior part of the internal capsule or corona radiata, is accompanied, as a rule, by impairment of vision in the opposite eye. This is no doubt due to interruption of the nerve fibres between the central terminations of the optic tract (corpora geniculata, optic thalamus, and tubercula quadrigemina) and the cere-

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* Leçons sur les Localisations dans les Maladies du Cerveau. Paris, 1878, pp 124, 125, 126.

† Ibid., pp. 119, 120, 121, 129.

bral convolutions. It is often unaccompanied by any perceptible alteration in the tissues of the eyeball or the optic nerves.

But it is not easy to account for blindness confined to the opposite eye, from lesions on one side of the brain, if each optic tract contains fibres destined for both eyes. We know that injury of one optic tract produces hemiopia in both eyes; and the only plausible explanation of this fact is in the supposed double distribution of its fibres. But it is equally certain that cerebral lesions of one side, above and behind the optic tracts, produce, on the contrary, blindness in the opposite eye. It is supposed by Charcot that a supplementary crossing may take place behind the central attachment of the optic tracts, like that indicated in Figs. 121 and 122. According to this view the crossed fibres of the right optic tract, which have come from the left eye, communicate with the right side of the brain; while its direct fibres, which have come from the right eye, cross the median line, perhaps in the tubercula quadrigemina, and communicate with the left side of the brain. Thus a region somewhere in the cortex of the left hemisphere will represent all the fibres coming from the right eye, and a corresponding region in the right hemisphere will represent all those from the left eye. This hypothesis still leaves some points of difficulty in regard to unilateral blindness and hemiopia, but it affords the most rational explanation of their principal phenomena.

In birds, the reflex stimulus which causes contraction of the pupil passes, owing to the complete decussation of their nerves, to the optic tubercle of the opposite side. But here, by the transverse connection of the parts, it becomes duplicated; and a beam of light, falling upon one retina, will produce contraction in both pupils. Even when one optic tubercle has been removed and the opposite eye permanently blinded, both pupils will contract under the stimulus of light falling upon the sound eye. In examining an eye, therefore, either in animals or in man, to determine whether it be sensitive to light, the opposite eye should always be covered, in order to prevent its exciting a movement by crossed reflex action.

Third Pair. The Oculomotorius.

The oculomotorius nerve, so called because it supplies most of the muscles moving the eyeball, originates from a collection of gray substance next the median line, beneath the tubercula quadrigemina and the aqueduct of Sylvius. As this group of nerve cells is continuous with that which gives origin to the fourth nerve or patheticus, it is designated as the *common nucleus of the oculomotorius and patheticus nerves.* From this nucleus the fibres of the oculomotorius pass downward and forward, through the crus cerebri, until they emerge, in the form of several flattened bundles, from its inner border, a little in front of the pons Varolii. They then unite into a rounded cord, which runs forward and outward, to penetrate the cavity of the orbit by the sphenoidal fissure. During this transit the nerve receives one or two twigs of sensitive fibres from the trigeminus. On entering the orbit, it divides into several branches, supplying the superior, inferior, and internal straight muscles of the eyeball, the inferior oblique, and the levator palpebræ superioris. The oculomotorius is accordingly concerned both in the vertical and lateral movements of the eyeball, and in those of rotation; while of the two other muscular nerves of this organ, the abducens is connected only with the movement of abduction, the patheticus only with that of rotation.

Decussation of the Oculomotorius Nerve.—According to Meynert, a decussation takes place between the oculomotorius nucleus and the opposite side of the brain by fibres crossing the median line in the raphe, near which the nucleus is situated. These fibres come originally from the corpus striatum, thence run backward along the inner border of the crus cerebri, and into the longitudinal lamina forming the raphe. Underneath the aqueduct of Sylvius they decussate at an acute angle, those from the right corpus striatum passing to the nucleus of the left side, and *vice versâ*. Each oculomotorius nerve is therefore in connection with the opposite side of the brain, not by means of its own fibres, but through the intervention of its nucleus and the fibres which pass thence, through the raphe, to the opposite corpus striatum.

Physiological Properties of the Oculomotorius Nerve.—The oculomotorius is in itself an exclusively motor nerve, and has been found by Longet, near its point of emergence from the crus cerebri, insensible to mechanical irritation; but at some distance farther forward, after receiving its branches of communication from the trigeminus, it exhibits a certain degree of sensibility. Its excitability, on the contrary, is very manifest; and its irritation within the cranial cavity, even after its separation from the brain, causes convulsive action in the muscles of the eyeball.

The physiological function of this nerve is shown by the paralysis following its section either before or after its entrance into the orbit. These results are for the most part simple and well marked, and are established by the uniform testimony of various observers. They consist of the paralysis of the five muscles to which the nerve is distributed, and induce, consequently;

1. *External strabismus*, from continued action of the external straight muscle of the eyeball, which is no longer antagonized by the internal.

2. *Immobility of the eyeball*, owing to the abolition of its upward, downward, lateral, and rotatory movements. For although two of the muscles of the eyeball, namely, the external rectus and the superior oblique, remain unparalyzed; yet, as they are no longer antagonized by the remainder, they can only produce a permanent deviation of the eyeball, but no alternate movement in different directions. In most of the lower animals there is also an unusual prominence of the eyeball, owing to paralysis of the retractor muscles.

3. *Drooping of the upper eyelid.* In the ordinary action of opening

the eye, it is the upper eyelid alone which moves, being raised to uncover the cornea and pupil, by the levator palpebræ superioris. As this muscle is animated by a branch of the oculomotorius, it is paralyzed by section of this nerve at the same time with the muscles moving the eyeball. The consequence is that the eye can no longer be fully opened; though it can be closed as usual by the action of the orbicularis oculi, which is supplied from the seventh pair. The eyelid therefore droops, resting in such a position as to cover the upper portion of the cornea, and the greater part or even the whole of the pupil. This condition is known as *ptosis*, and is one of the consequences following paralysis of the oculomotorius nerve.

The influence of the oculomotorius on the *contractile movements of the iris* is important, though less distinct and uniform than that exerted on the movements of the eyeball. The connection of the oculomotorius with the muscular apparatus of the iris is indirect, taking place through the intervention of the ophthalmic ganglion, to which it sends a motor branch, and which in turn gives off the ciliary nerves for the iris. Some observers (Mayo, Longet) have found well-marked paralysis of the iris following division of the oculomotorius nerve, and enumerate, as consequences of this injury, permanent dilatation and immobility of the pupil. In the experiments of Longet, on dogs, rabbits, and pigeons, irritation of the cephalic extremity of the optic nerve caused contraction of the pupil in both eyes; but after division of the oculomotorius nerve the effect was no longer produced on the operated side. Bernard has also found that division of the oculomotorius is followed, in the rabbit, by dilatation of the pupil, and that in the operated eye the iris contracts only very slowly and imperfectly under the influence of light. It is not, however, completely paralyzed, since it may still move with considerable promptitude under the influence of painful impressions conveyed by the fifth pair. The action of the oculomotorius on the pupil, therefore, is energetic and constant in the ordinary reflex movement of contraction under the stimulus of light; but it takes place through the ophthalmic ganglion, to which it communicates, in a certain degree, its motive power.

Fourth Pair. The Patheticus.

This nerve presents certain peculiarities, which, notwithstanding its minute size, have attracted to it special attention. It is distributed exclusively to the superior oblique muscle of the eyeball; its name having been derived from the erroneous idea that this muscle turned the eye upward and inward. Both the superior and inferior oblique muscles, however, have been fully shown to cause in the eyeball a nearly simple movement of rotation about its longitudinal axis. They are antagonistic to each other; and by their contraction and relaxation, during movements of inclination of the head from side to side, they maintain the horizontal planes of the eyeballs in the same position. If this parallelism were not preserved, objects would appear to stand in different degrees of obliquity to the two eyes, producing uncertainty and double vision.

The apparent origin of the patheticus nerve is immediately behind the tubercula quadrigemina, on the upper surface of the *valve of Vieussens,* a thin lamina of white substance, covering the anterior part of the fourth ventricle. The root fibres of the nerve, however, can be traced transversely through the substance of the valve. According to Henle and Meynert, a great part cross the median line, decussating with those from the corresponding nerve on the opposite side; then, turning downward and forward, they reach a collection of gray matter just behind the nucleus of the oculomotorius nerve, and continuous with it. According to Henle, a portion of the fibres also terminate, without crossing the median line, in the nucleus of the same side. The nucleus is situated beneath the aqueduct of Sylvius and the anterior tubercula quadrigemina; while the point of exit of the nerve is above the aqueduct of Sylvius and behind the posterior tubercula quadrigemina. Its root fibres, accordingly, after leaving their nucleus of origin, encircle the walls of the aqueduct, running obliquely upward and backward, and then crossing the median line to their emergence on the opposite side.

From this point, the nerve passes forward, as a slender filament, not more than one millimetre in diameter, along the upper wall of the cavernous sinus, where it lies in immediate proximity to the oculomotorius; and thence, entering the cavity of the orbit by the sphenoidal fissure, terminates in the superior oblique muscle of the eyeball.

The course of the oculomotorius and patheticus, when compared, shows a remarkable relation between the two nerves. Their fibres originate from adjacent portions of the same nucleus. Those of the oculomotorius pass downward and forward, to emerge from the inner border of the crus cerebri, at the base of the brain; while those of the patheticus pass upward and backward, emerging from the valve of Vieussens, between the cerebrum and cerebellum. But the nerves afterward run side by side, in their passage toward the orbit, and are finally distributed to muscles associated in the movements of the same organ.

Physiological Properties of the Patheticus Nerve.—The distribution of this nerve to a muscle which receives filaments from no other source indicates in great measure its motor character, which is furthermore established by the results of observation. The experiments of Chauveau on the horse and rabbit, and those of Longet on the horse, ox, and dog, show that galvanization of this nerve within the cranium produces contraction of the superior oblique muscle, with rotation of the eyeball on its longitudinal axis from without inward; and in those of Longet there was also a deviation of the pupil outward. In cases quoted by Longet, attributed to paralysis of this nerve, in man, there was incapacity of rotation of the eyeball on the affected side, and consequently double vision, the image perceived by the affected eye being oblique and inferior in regard to the other; but these disturbances of vision disappeared when the head was inclined toward the opposite side.

The patheticus is, accordingly, the motor nerve of the superior oblique muscle, and acts in harmony with the oculomotorius to preserve the horizontal plane of the eyeball.

Fifth Pair. The Trigeminus.

The fifth pair occupies, in every respect, a prominent place among the cranial nerves. It is the great sensitive nerve of the face, being the only source of general sensibility for the integument and mucous membranes of this region; and, by branches of communication to the corresponding motor nerves, it provides for the imperfect sensibility of the facial muscles. But while in its main portion it is preëminently sensitive, it also possesses motor fibres, derived from a distinct root, and distributed to muscles of a special group. Before emerging from the cranial cavity it separates into three main divisions, destined for the corresponding regions of the face; and its name, trigeminus, is derived from the fact that in man these three primary divisions are nearly alike in size and importance.

The apparent origin of the fifth nerve is from the lateral portion of the pons Varolii, where its two roots emerge in close approximation to each other, but usually separated by a narrow band of the transverse fibres of the pons. The anterior or motor root is the smaller of the two, being about two millimetres in diameter; the posterior or sensitive root is the larger, having a diameter of about five millimetres. Both roots may be traced, through the pons Varolii, backward, upward, and inward, to the gray substance beneath the anterior part of the fourth ventricle. During the greater part of this passage they remain distinct, but join each other above and become closely entangled by the interweaving of their bundles; though their fibres may still be distinguished, on microscopic examination, by the generally larger size of those belonging to the motor root. They finally reach a collection of gray substance, the "trigeminal nucleus," situated next behind that of the oculomotorius and patheticus, but farther outward from the median line, occupying the extreme lateral part of the fourth ventricle, where its floor forms an angle with the roof. The fibres of the nerve terminate partly in or among the large, stellate, and dark-colored cells of this nucleus. According to Henle, a portion also pass through the nucleus, and across the median line to the opposite side; the two sets together forming, in this way, partly a direct and partly a crossed connection between the peripheral organs and the nervous centres.

After emerging from the pons Varolii, the two roots of the fifth nerve pass outward and forward in company with each other, the larger, posterior, or sensitive root being placed above, the smaller, anterior, or motor root underneath. At the apex of the petrous portion of the temporal bone, a little outside and behind the posterior clinoid process of the sella turcica, the fibres of the sensitive root spread out into a network of inosculating bundles, in the substance of the *Gasserian ganglion.* This ganglion forms a flattened, crescentic mass of gray substance, mingled with the fibres from the sensitive root. The ganglionic cells are unipolar in form, giving off fibres in a peripheral direction, which, according to Key and Retzius, unite with those of cerebral origin in the sensitive root. The motor root passes beneath the ganglion as a distinct bundle, neither giving nor receiving any communicating fibres. At the anterior border of the ganglion, the nerve separates into its three bundles, namely, the first, or ophthalmic; the second,

Fig. 123.

Diagram of the Fifth Nerve and its Distribution.—1. Sensitive root. 2. Motor root. 3. Gasserian ganglion. I. Ophthalmic division. II. Superior maxillary division. III. Inferior maxillary division. 4. Supra-orbital nerve, distributed to the skin of the forehead, inner angle of the eye, and root of the nose. 5. Infra-orbital nerve; to the skin of the lower eyelid, side of the nose, and skin and mucous membrane of the upper lip. 6. Mental nerve; to the integument of the chin and edge of the lower jaw, and skin and mucous membrane of the lower lip. *n, n.* External terminations of the nasal branch of the ophthalmic division; to the mucous membrane of the inner part of the eye and the nasal passages, and to the base, tip, and wing of the nose. *t.* Temporal branch of the superior maxillary division; to the skin of the temporal region. *m.* Malar branch of the superior maxillary division; to the skin of the cheek and neighboring parts. *b.* Buccal branch of the inferior maxillary division; passing along the surface of the buccinator muscle, and distributed to the mucous membrane of the cheek, and to the mucous membrane and skin of the lips. *l.* Lingual nerve; to the mucous membrane of the anterior two-thirds of the tongue. *at.* Auriculo-temporal branch of the inferior maxillary division; to the skin of the anterior part of the external ear and adjacent temporal region. *x, x, x.* Muscular branches; to the temporal, masseter, and internal and external pterygoid muscles. *y.* Muscular branch; to the mylo-hyoid and anterior belly of the diagastric. *f.* Sensitive branch of communication to the facial nerve.

or superior maxillary; and the third, or inferior maxillary divisions of the trigeminus.

The *ophthalmic division* passes through the sphenoidal fissure into the orbit of the eye, where it gives filaments to the ophthalmic ganglion and to the eyeball; a nasal branch, supplying the integument and mucous membrane of the inner part of the eye, the mucous membrane of the middle and inferior nasal passages, and the integument of the root, wing, and tip of the nose; and a branch to the lachrymal gland and the integument of the upper eyelid and adjacent region. It then emerges from the orbit by the supra-orbital notch, and is distributed to the skin of the forehead and side of the head, as far back as the vertex.

The *superior maxillary division* passes through the foramen rotundum into the spheno-maxillary fossa, where it gives a sensitive branch to the spheno-palatine ganglion of the sympathetic, thence through the longitudinal canal in the floor of the orbit, where it gives off a branch running upward and outward to the skin of the malar and temporal regions, and numerous descending branches to the teeth, gums, and adjacent mucous membrane of the upper jaw, and to that of the inferior nasal passages. It then emerges upon the face by the infra-orbital foramen, and is distributed to the integument of the lower eyelid and the side of the nose, and to the skin and mucous membrane of the upper lip.

The *inferior maxillary division* leaves the anterior border of the Gasserian ganglion at a different angle from the two others, passing almost vertically downward through the foramen ovale. This division receives all the fibres of the motor root, which become more intimately united with it during its passage through the base of the skull. While the two other divisions of the fifth nerve are therefore exclusively sensitive, the inferior maxillary division is a mixed nerve, containing both motor and sensitive fibres.

After supplying one or two filaments to the otic ganglion of the sympathetic, and while passing down toward the inferior dental canal, it gives off two sensitive branches, namely, 1st, the buccal (Fig. 123, *b*) to the mucous membrane of the cheek, and the skin and mucous membrane of the lips; and 2d, the *auriculo-temporal* branch (*at*), which turns backward and upward, to be distributed to the integument of the anterior wall of the external auditory meatus, the anterior part of the external ear, and the adjacent temporal region. From this branch a twig of considerable size (*f*) turns forward to join the facial nerve, communicating to its branches in front of this point a perceptible degree of sensibility.

Another sensitive branch of this portion of the nerve is the *lingual* (*l*), which sends filaments to the submaxillary gland, the sympathetic submaxillary ganglion, and adjacent mucous membrane of the mouth, and is mainly distributed to the mucous membrane and papillæ of the tip, edges, and surface of the anterior two-thirds of the tongue. The *motor* branches are those (x, x, x) going to the temporal, masseter, and two pterygoid muscles, and that distributed (y) to the mylohyoid muscle and the anterior belly of the digastric.

The remaining portion of the trigeminus then enters the dental canal of the inferior maxilla, through which it passes, giving off filaments to the teeth and gums of the lower jaw. It finally emerges at the mental foramen, and is distributed in numerous diverging ramifications to the integument of the chin and edge of the under jaw, and the skin and mucous membrane of the lower lip.

Physiological Properties of the Fifth Pair.—The most prominent character of this nerve is its *general sensibility.* The regions to which it is distributed, namely, the cheeks, eyelids, tip of the nose, lips, anterior nares, and especially the tip of the tongue, possess a tactile sensibility of higher grade than most other parts of the body. The nerve itself, together with its principal branches, is acutely sensitive to mechanical irritation, and will give rise to indications of sensibility under conditions when the spinal nerves are nearly or quite inactive.

But the most direct and conclusive proof of the function of this nerve is the loss of sensibility produced by its division. If either the infraorbital or the mental branch be divided at its exit from the superior or inferior maxilla, tactile sensibility is impaired or abolished in the corresponding region of the face. A still more striking result is produced by dividing the entire nerve within the cranium. This operation, which was first performed by Magendie, may be done, upon the cat or the rabbit, by means of a steel instrument with a slender shank and a narrow cutting blade projecting at nearly a right angle from its extremity. The instrument is introduced in a horizontal direction through the squamous portion of the temporal bone, and pushed inward and forward, with its blade lying flatwise on the floor of the skull, until it strikes the posterior clinoid process. It is then slightly withdrawn, its cutting edge turned downward, and the nerve divided where it crosses the petrous portion of the temporal bone. By this method all its fibres are cut off, and the only part of the brain necessarily wounded is the inferior portion of the temporal lobe.

The immediate effect of this operation is a complete anæsthesia of the integument and mucous membranes about the face on the operated side. The cornea can be touched without exciting any movement of the eyelids. A probe may be introduced into the nasal passages, or the lips may be pierced with a needle, without eliciting any sign of sensation on the part of the animal. At the same time the power of motion in these parts is unaffected. The eyelids may be opened or closed under the influence of visual impressions, and the movements of the lips continue to be performed in a nearly natural manner. In the cat, the loss of sensibility and persistence of the power of motion is shown by irritating at different points the integument of the external ear, which in this animal has an acute tactile sensibility. If a pointed instrument be brought in contact, on the operated side, with the anterior part of the ear, which is supplied by fibres from the third division of the fifth nerve, no effect is produced. But if the same irritation be applied to the back part of the ear, which is supplied by the great auricular nerve from the cervical plexus, a twitching movement is at once excited. According to Longet, the most violent injuries, such as exsection of the eyeball, evulsion of the hairs about the lips, extraction of the teeth, or destruction of the integument by the actual cautery, may be performed, after complete division of the fifth nerve, without causing any painful sensation.

The fifth pair is accordingly the exclusive source of sensibility in the superficial regions of the face, and all parts of the nasal and buccal cavities to which it is distributed.

Painful Affections of the Fifth Pair.—This nerve is also the seat of neuralgic affections about the head and face. The most common of these is *headache;* which may be general, extending over the whole forehead and vertex, or confined to one side. It often seems to be located in the branches supplying the periosteum, especially of that lining the orbit and the frontal sinuses. Where the pain is deep-seated, its location may be in the dura mater or the bones of the skull; since each division of the fifth pair, either before or immediately after leaving the cavity of the cranium, sends a slender recurrent branch to the dura mater and the cranial bones. That from the ophthalmic division may be traced into the tentorium, in which it ramifies as far as the sinuses bordering its attached edge.

Toothache, from irritation of the dental filaments of the fifth pair, is generally due to decay of the dentine, and consequent exposure of the tooth pulp to mechanical injury. Neuralgia of the teeth may also be caused, like headache, by indigestion, exposure, or fatigue; the pain existing simultaneously in several teeth, without morbid alteration of their structure.

The most severe and persistent form of neuralgia in this nerve is *tic douloureux;* habitually located in one of its three principal divisions as they emerge upon the face. The pain is usually intermittent, recurring in great severity at various intervals, and lasting but a few minutes at a time. It is most frequently seated in the upper and middle regions of the face, corresponding with the distribution of the supra and infraorbital nerves.

Lingual Branch of the Fifth Pair.—This branch, known as the "lingual nerve," communicates to the mucous membrane of the tongue its tactile sensibility. This sensibility is highly developed in the anterior two-thirds of the tongue, and at its tip is more acute than in any other region of the body. It disappears completely on the operated side, when the fifth nerve has been divided within the cranium; and after section of both lingual nerves, according to Longet, it is lost in the whole anterior two-thirds of the organ. The tactile sensibility of the tongue is of great importance in man and many animals, as an aid in mastication, for appreciating the physical qualities of the food, to perceive when it is reduced to the proper consistency for swallowing, and to detect any remnants left among folds or crevices of the mucous membrane.

The lingual nerve is also endowed with the special sensibility of *taste.* This function is difficult to investigate in animals, owing to the uncertainty of its indications, and the difficulty of isolating separate regions of the cavity of the mouth. Experiments upon man, which are made with comparative facility, have been performed by Guyot, Vernière, Dugès, and Longet in such a manner as to leave no doubt that the sense of taste is highly developed in those portions of the tongue exclusively supplied by the lingual nerve. They consist mainly in applying to different parts of the mucous membrane a pellet of lint, moistened with a solution of some substance, like quinine or colocynth, possessing a distinct taste without irritating qualities. In this way it is ascertained that the point, edges, and upper surface of the tongue, throughout its anterior two-thirds, is capable of perceiving sensations of taste, without aid from other parts of the mucous membrane. According to the experiments of Bernard and Longet on animals, division of the lingual nerve destroys the faculty of taste as well as that of general sensibility in the corresponding parts of the tongue; and similar observations are quoted by Henle, after section of this nerve in man.

Muscular Branches of the Fifth Pair.—These branches, which are all given off from the inferior maxillary division of the nerve, are distributed to the temporal, the masseter, and the external and internal pterygoid muscles, as well as the mylohyoid muscle and the anterior belly of the digastric. They are all therefore concerned in the movements of mastication. The most powerful of the muscles to which they are distributed, namely, the temporal and the masseter, act by bringing the teeth of the lower jaw forcibly in contact with those of the upper. The action of the pterygoid muscles produces a lateral grinding movement, by which the trituration of the food is accomplished; and finally those supplied by the mylohyoid branch act by opening the jaws, to allow a repetition of the former motions. In different animals these movements vary in relative importance. In the carnivora, the closure of the jaws preponderates over the rest, enabling the animal to seize and retain his prey. In the herbivora, the lateral grinding movements are more important for comminuting the seeds, grains, vegetable fibres and other hard substances upon which they feed. In man, both movements exist in a nearly equal degree.

Anastomotic Branches of the Fifth Pair.—Although the superior, middle, and inferior regions of the face are respectively supplied, in general, by the three great divisions of this nerve, there is yet more or less communication between adjacent branches, so that each region receives fibres from different sources. Thus the infraorbital nerve, which sends filaments to the lower eyelid, inosculates with a branch of the ophthalmic division. The integument of the nose is supplied by the nasal branches of the ophthalmic division, and also by those coming from the infraorbital nerve. The upper and lower lips are both supplied from the infraorbital and mental nerves on the outside, and from the terminal filaments of the buccal nerve on the inside; and the temporal region receives branches both from the superior and inferior maxillary divisions. A most important anastomotic branch is that to the facial nerve (Fig. 123, *f*), which it supplies with sensitive filaments. Many of these filaments no doubt terminate in the facial muscles, to which they communicate a certain amount of sensibility; but there are also abundant anastomoses between the facial nerve and the fifth near their final distributions, and certain regions of the integument may be supplied with sensibility from this source. The observations of L'Etiévant * show that it is impossible, in man, to abolish completely the sensibility of any extended region of the face by section of a single division of the fifth pair; some degree of sensibility still remaining, due to inosculatory filaments from other divisions of the nerve, either directly or through the branches of the facial.

According to Henle, there is still a portion of the side of the face which may derive sensibility from the great auricular nerve of the cervical plexus; since the anterior branch of this nerve, after supplying the under part of the lobe of the ear, sends some slender filaments forward to the integument of the cheeks, in some instances as far as the neighborhood of the malar bone.

Influence of the Fifth Pair on the Special Senses.—This nerve has an important connection with the special senses, since they are more or less impaired, and in some instances practically destroyed, by its division or injury. Its influence, however, is mainly indirect; showing itself for the most part by disturbance of nutrition in the tissues of the organ after the nerve has been cut off. These effects seem to depend, not on the division of the ordinary sensitive fibres of the nerve, but on that of sympathetic fibres derived from the Gasserian ganglion, or supplied, through its branches, to the organs of sense.

Influence on the Sense of Smell.—The nasal passages are supplied by two different cerebro-spinal nerves, namely, the olfactory nerve, distributed to their upper portions, and endowed with special sensibility; and the nasal branches of the fifth pair, distributed in the lower portions, to which they communicate general sensibility. The mucous membrane also contains filaments from the spheno-palatine ganglion of the sympathetic; which, in turn, receives its sensitive root from the superior maxillary division of the fifth pair.

The general sensibility of the nasal passages may accordingly remain after the sense of smell has been destroyed. But if the fifth pair be divided, not only is general sensibility abolished in the nasal mucous membrane, but there is also a disturbance in its nutrition, which destroys the power of smell. The membrane becomes swollen, and the passages are obstructed by accumulation of mucus. According to

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* Traité des Sections Nerveuses. Paris, 1873, p. 179.

Longet, the membrane also assumes a fungous consistency, and is liable to bleed at the slightest touch. It is owing to a similar condition that the power of smell is impaired in nasal catarrh or influenza. The olfactory nerves become inactive in consequence of the morbid alteration in their mucous membrane and its secretions.

Influence on the Sense of Sight.—The anterior parts of the eyeball are provided with nerves of ordinary sensibility from the fifth pair; while impressions of light are transmitted exclusively by the optic nerve. The iris and cornea are furthermore supplied by filaments from the ophthalmic ganglion of the sympathetic, which receives its sensitive root from the fifth pair. If this nerve be divided either in front of or through the Gasserian ganglion, the cornea often becomes the seat of congestion and ulceration, sometimes resulting in complete destruction of the eye. Immediately after the operation the pupil is contracted and the conjunctiva loses its sensibility. At the end of twenty-four hours the cornea is opaline, and by the second day the conjunctiva is congested, and discharges a purulent secretion. As the process increases in intensity, the cornea grows more opaque, until it becomes quite impermeable to light, and vision is consequently suspended. In some cases there is at last sloughing and perforation of the cornea and discharge of the humors of the eye; in others, after a few days, the inflammatory appearances subside, and the eye is gradually restored to its natural condition.

According to Bernard, these effects are either retarded or wanting when the nerve is divided behind the Gasserian ganglion. This indicates that its influence on the nutrition of the eyeball does not reside in the fibres of its own roots, but in additional filaments derived from the ganglion.

Influence on the Sense of Taste.—The lingual branch of the fifth pair communicates to the anterior portion of the tongue both its general sensibility and the faculty of taste; both of which are abolished by its division. It is probable that these two kinds of sensibility reside in different nerve fibres; since cases have been observed in which the sense of taste is diminished or lost while the tactile sensibility of the tongue remains unimpaired. It has not been possible thus far to determine the special source or location of the two functions in the lingual nerve; but it is evident that the exercise of taste is facilitated by the general sensibility of the tongue, and is influenced by the condition of the local circulation and the buccal secretions. When the tongue is dry and coated from febrile action the taste is either abolished or replaced by morbid sensations. It depends therefore for its exercise, not only on the special sensibility of the lingual nerve, but also on all the conditions requisite for the integrity of the mucous membrane.

Influence on the Sense of Hearing.—The influence of the fifth pair on the perception of sound is less distinct than in regard to the other special senses, and is only surmised from its anatomical relations. It provides for the general sensibility of the external ear by twigs from its auriculo-temporal branch, which supply the anterior border of the concha and the anterior wall of the external auditory meatus. Its relation with the deeper parts of the organ is established through the otic ganglion of the sympathetic, which receives a few fibres from its inferior maxillary division, and sends a filament backward to the plexus on the inner surface of the membrane of the tympanum. This plexus is also supplied with filaments from the ganglion of the glosso-pharyngeal nerve; and is consequently made up of fibres from both these sources. Its sensitive fibres terminate in the lining membrane of the middle ear. The secretions, both of this cavity and of the external auditory meatus, are important for the preservation of the integrity of the parts and for the mechanism of audition; and a considerable portion of their nervous supply is derived from the fifth pair.

Sixth Pair. The Abducens.

The abducens nerve, so called because it is distributed to the single muscle causing abduction of the eyeball, originates mainly from a deposit of gray substance on the floor of the fourth ventricle near its widest part, at a point corresponding with the posterior border of the pons Varolii. It is situated next the median line, and is indicated on each side by a longitudinal prominence, known as the "fasciculus teres." This nucleus is designated as the *common nucleus of the abducens and facial nerves;* since the root fibres of both these nerves are traced, through somewhat different routes, to its gray substance. The fibres of the abducens, as shown by Dean, Meynert, and Henle, originate from the inner border of the nucleus without apparent decussation with those of the opposite side. They pass almost directly downward and forward, through the tuber annulare, to their emergence at the base of the brain, at the posterior edge of the pons Varolii. From this point, the nerve, which is about two millimetres in thickness, runs forward, beneath the pons, passing, in company with the oculomotorius and patheticus, along the wall of the cavernous sinus and through the sphenoidal fissure, to the cavity of the orbit, where it terminates in the external straight muscle of the eyeball.

Physiological Properties of the Abducens.—By the experiments of Longet on rabbits, and those of Chauveau on rabbits and horses, the abducens is shown to be, at its origin, exclusively a motor nerve; since its irritation in this region produces contraction of the external straight muscle of the eyeball, without any indication of sensibility. According to Longet, the difference in this respect between the abducens and the trigeminus is very marked; irritation of the trigeminus always giving rise to signs of acute sensibility, while that of the abducens has no other effect than local muscular contraction.

Division of this nerve causes internal strabismus from paralysis of the external straight muscle, and loss of the power of horizontal rotation of the eyeball; while its vertical movements are still preserved, owing to the continued activity of the oculomotorius nerve. There are cases of internal strabismus, in man, accompanied by the above symptoms, apparently due to compression of the abducens nerve within the cranial cavity.

Seventh Pair. The Facial.

In the innervation of the external parts of the face, this nerve holds an equal rank with the fifth pair, and may be regarded as complementary to it in physiological endowments. As the trigeminus is the nerve of sensation for the integument of this region, the facial is the motor nerve for its superficial muscles. It is the nerve of expression, by which the features are animated in their varying movements, corresponding with the different phases of mental or emotional activity. Although at its origin an exclusively motor nerve, it receives, soon after its emergence from the cranium, a communicating branch from the fifth pair, which gives to it, and to the muscles in which it terminates, a certain share of sensibility.

The facial nerve has its principal source in a collection of gray substance, already described as giving origin to the abducens (page 467). The fibres of the abducens and facial nerves are given off from its internal and external borders respectively; those of the abducens passing directly downward through the tuber annulare, near the median plane, those of the facial first passing outward and then bending downward, to their point of emergence at the lateral part of the posterior edge of the pons Varolii.

According to Dean, Meynert, and Henle, a considerable portion of the root fibres of the facial nerve communicate, either directly or through the nucleus, across the median line, with the opposite side of the brain.

After emerging from the edge of the pons Varolii, the facial nerve, in company with the auditory, passes into and through the internal auditory meatus. It thence enters the aqueduct of Fallopius, and, following the course of this canal through the petrous portion of the temporal bone, comes out at the stylomastoid foramen and turns forward upon the side of the face. It spreads out between the lobules of the parotid gland in a number of branches, which, by mutual interlacement, form the well-known "parotid plexus," or "pes anserinus," of this nerve. Its branches thence diverge upward, forward, and downward, to the superficial muscles of the facial region. It also supplies, by branches given off immediately after its emergence from the stylomastoid foramen, the muscles of the external ear, as well as the stylohyoid and the posterior belly of the digastric; and by a twig which descends to the submaxillary region, it supplies filaments to the upper part of the platysma myoides, and communicates with an ascending branch of the superficial cervical nerve from the cervical plexus.

Physiological Properties of the Facial Nerve.—The facial is shown, by the result of abundant investigations, to be, at its origin and in its main physiological characters, a motor nerve. Not only is the tactile sensibility of the facial region completely destroyed by section of the trigeminus, though the facial remain uninjured, but, according to both Magendie and Bernard, the trunk of the facial, when irritated at its source within the cranial cavity, exhibits no sign of sensibility, although that of the fifth pair may be at the same time perfectly manifest. On the other hand, Chauveau has found that in the recently killed animal, galvanization of the intracranial portion of the facial nerve causes contraction of the muscles of the face and of the external ear. The nerve is accordingly, at its source, excitable, but insensible.

Fig. 124.

Diagram of the Facial Nerve and its Distribution.—1. Facial nerve at its entrance into the internal auditory meatus. 2. Its exit, at the stylomastoid foramen. 3, 4. Temporal and posterior auricular branches, distributed to the muscles of the external ear and to the occipitalis. 5. Branches to the frontalis muscle. 6. Branches to the stylohyoid and digastric muscles. 7. Branches to the upper part of the platysma myoides. 8. Branch of communication with the superficial cervical nerve of the cervical plexus.

Furthermore, the most decisive results are obtained from division of the facial nerve at various parts of its course. This may be done, in quadrupeds, at its point of exit from the stylomastoid foramen, or, as practised by Bernard, during its passage through the aqueduct of Fallopius, by a cutting instrument introduced into the cavity of the tympanum, and reaching the nerve through its upper wall. This section paralyzes all the superficial muscles of the face on the corresponding side. The visible effects vary in the different facial regions, according to the function of the paralyzed muscles.

Effect on the Eye.—Owing to paralysis of the orbicularis oculi, the eye on the affected side cannot be closed; according to Bernard it remains open even while the animal is asleep. This depends on the fact that the muscles serving to open and close the eyelids are animated by different nerves; the levator palpebræ superioris, which lifts the upper eyelid, being supplied by the oculomotorius, while the orbicularis oculi receives its filaments from the facial. In paralysis of the facial, therefore, complete closure of the lids is impossible, although the movements of the eyeball and pupil are unaffected.

At the same time the movement of winking is suspended on the affected side. This is a reflex action, caused by the contact of air with the surface of the cornea, and the accumulation of tears along the edge of the lower eyelid. At short intervals this excites a momentary contraction of the orbicularis, by which the eyelids are brought together, and again immediately separated; thus spreading the lachrymal secretion uniformly over the cornea and protecting it from desiccation. After section of the facial nerve, this movement ceases; and if a solid body be suddenly thrust toward the face of the animal, the eye on the sound side instinctively closes, while the other remains open. Even touching the cornea on the operated side fails to cause contraction of the eyelids, although the animal shrinks and the eyeball turns in its orbit; showing that sensibility remains, although the motor power of the orbicularis is lost.

Precisely opposite effects, accordingly, are produced by section of the fifth nerve, and by that of the facial. After division of the fifth, touching the cornea fails to produce closure of the eyelids because the sensibility of the surface has been destroyed, though the power of motion remains. When the facial has been divided, muscular action is paralyzed, and sensibility remains entire.

Effect on the Nostrils.—In man, as well as in some animals, the nostrils are nearly motionless in the ordinary state of respiration. They expand, however, with considerable vigor when the breathing is increased in frequency, or when the air is forcibly inspired to assist the sense of smell; and in many quadrupeds they exhibit regular movements of expansion and collapse, synchronous with those of the chest and abdomen. In man, this action becomes very marked whenever the breathing is hurried or laborious, owing to muscular exertion or obstruction of the air-passages.

These movements are suspended by section of the facial nerve. The nostril on the affected side becomes flaccid, and, instead of opening for the admission of air, it collapses and forms an obstruction to its entrance. As the dyspnœa thus induced tends to accelerate respiration, the paralyzed nostril is still further compressed in inspiration; and at expiration it is forcibly extruded by the outgoing current. The natural movements of the nostril are therefore reversed by paralysis of the facial nerve. In the normal condition it expands in inspiration, and partially collapses in expiration. But after section of the nerve it collapses in inspiration, and partially opens in expiration; moving passively, like an inert valve, with the changing direction of the air current.

Effect on the Lips.—In animals, and especially in the herbivora, the movements of the lips serve mainly for prehension of the food; and if they be paralyzed on both sides, the consequent incapacity to introduce food into the mouth may be sufficient to cause death by inanition. In the carnivora the retraction and elevation of the lips, by which the canine teeth are uncovered, have a marked effect on the expression of the face; and in most animals, after division of the facial nerve, the change of appearance in the corresponding side, even in the quiescent condition, is distinctly perceptible. The lips are inactive, and the corner of the mouth hangs down partly open, owing to paralysis of the orbicularis oris.

Effect on the Ears.—In many quadrupeds the external ears are more important than in man, owing to their greater development and superior mobility. Their varying position has great influence in modifying the expression; and their rapid and extensive movements are of essential aid in the sense of hearing. When the facial nerve has been divided, the ear on the corresponding side becomes motionless; and if long and narrow, as in the rabbit, it can no longer maintain the erect position.

Facial Paralysis in Man.—Facial paralysis, from disease involving the trunk of the nerve, or its sources in the brain, is not an uncommon affection in man. It is usually confined to one side, being limited by the median line, and producing a difference of expression on the two sides of the face. Where the difficulty is located in particular branches of the nerve, certain portions of the face may be affected to the exclusion of others. The lips may be paralyzed without loss of motion in the parts above, and *vice versâ;* or the affection may be fully developed in one region, and only partial in the remainder. But when the disease is seated on the trunk of the nerve, within the aqueduct of Fallopius, or involves its central origin, its consequences extend uniformly over one side, forming a complete unilateral facial paralysis.

The signs of facial paralysis in man are, in general, those which follow experimental division of this nerve in animals. Its main peculiarity depends on the greater development, in man, of the facial muscles as organs of expression; and its most marked effect is consequently loss of expression on the paralyzed side. All the features have a collapsed appearance. The eyelids are motionless, the eye remains constantly open, and the lower lid sinks below the level of the cornea; thus giving to the eye a staring, vacant appearance. The act of winking is no longer performed on the affected side. Owing to the paralyzed condition of the frontalis and superciliary muscles, all the characteristic lines and wrinkles on this side disappear, and the forehead and eyebrow become smooth and expressionless. The same is true of the cheek, which, as well as the nostril, is flattened and collapsed. The corner of the mouth hangs downward, and owing to imperfect closure of the lips there is sometimes a continual escape of saliva from this point.

Beside these symptoms there is also a *deviation of the mouth toward the sound side*, owing to the facial muscles on that side being no longer antagonized by the opposite. In many instances this deviation is not observable during a state of quiescence, both sets of muscles being habitually relaxed; and it becomes evident only when the patient uses those of the sound side, as in speaking, whistling, or laughing, or when the emotions are excited. But in cases where the face has naturally an abundance of expression, the distortion of the features, and their different appearance on the two sides, are distinct at all times, becoming still more marked when the patient is excited or engaged in conversation.

Fig. 125.

Facial Paralysis of the right side.

Another effect of facial paralysis in man is *difficulty in drinking and in mastication.* The difficulty in drinking is due to deficient action of the orbicularis oris on the affected side; so that the lips at this corner of the mouth cannot be kept in contact with the sides of the goblet.

The fluid consequently escapes and runs over the lower part of the face, unless the patient aids the paralyzed part by pressure with the fingers. The difficulty in mastication results from paralysis of the buccinator muscle, and the relaxed condition of the cheek. The food consequently lodges between the gum and the cheek; and the patient is often obliged to remove it by mechanical means in order to complete its mastication.

The loss of power in the orbicularis also produces *imperfect articulation.* The lips cannot be brought together with precision, and the labials, such as B and P, are imperfectly pronounced. In cases of bilateral paralysis, which have been sometimes observed, the features are no longer deviated from their symmetrical position, but the difficulty of articulation is much increased, extending to some of the vowels, such as O and U, which require contraction of the orbicularis oris. This affection is distinct from that known as "glosso-labio-laryngeal paralysis" (page 445), in which articulation is also impaired. In the latter disease, which is of central origin, the paralysis affects the muscles of the tongue and larynx, as well as those of the lips; in facial paralysis it is confined to those which receive their filaments from the seventh pair. Facial paralysis may therefore exist without danger to life.

Crossed Action of the Facial Nerve.—Minute examination of the origin of this nerve indicates a transverse communication by decussating fibres, between its nucleus on the floor of the fourth ventricle and the opposite side of the tuber annulare. It has not yet been found possible, however, to follow these fibres throughout, or to decide whether they are root fibres which have simply passed through the nucleus, or whether they originate from the nerve cells of the nucleus and thence pass to the opposite side.

That the facial nerve has in great part a crossed action is evident from the results of pathological observation. Facial paralysis is a frequent accompaniment of hemiplegia; and in the great majority of instances, that is, when the cerebral lesion is above the tuber annulare, the hemiplegia of the body and limbs and the paralysis of the face are on the same side with each other. The injury to the brain, therefore, in such cases, produces both hemiplegia and facial paralysis on the opposite side. But when the injury is lower down, in the tuber annulare, it may affect at the same time the roots of the facial nerve outside its nucleus, and the anterior pyramids above their decussation; causing in this way a facial paralysis on the same side and hemiplegia on the opposite side. It thus appears that the facial paralysis is on the side of the cerebral lesion when this is below the nucleus, and on the opposite side when it is above the nucleus or in the hemispheres. This shows that the action of the facial nerve is largely a crossed action.

The cross connection, however, between the nucleus and the opposite side of the brain does not affect all the functions of this nerve. The only decussation of its fibres known to exist is that which takes place at the raphe on the floor of the fourth ventricle. If all the fibres of the nerve root crossed at this point, a longitudinal section at the median line between the two nuclei would completely paralyze both sides of the face. But this effect is not produced; since in the experiments of Vulpian,* on dogs and rabbits, the animals after this operation were still capable of winking with both eyes; only the action was no longer simultaneous, each eye being closed at irregular intervals independently of the other.

It is evident, therefore, that the reflex action, in winking, takes place for each eye on the same side, no doubt in the gray substance of the facial nucleus; the two nuclei habitually acting in harmony by means of their commissural fibres. But the voluntary and emotional impulses, which cause movement of the features, are transmitted by decussating fibres from opposite sides of the brain.

This is still further indicated by the effects of peripheral and central lesions of the nerve. In man, as well as in animals, if this nerve be divided or destroyed during its passage through the aqueduct of Fallopius, all the facial movements are paralyzed together. But in paralysis depending on a cerebral lesion above the nucleus, it is generally observed that the loss of motion is not complete; but that, while all other movements of the face are paralyzed, the action of winking remains on the affected side. This peculiarity is used as a means of diagnosis between facial paralysis from injury of the nerve and that caused by a lesion in the brain.

Sensibility of the Facial Nerve.—Although this nerve is exclusively motor at its origin, it subsequently receives filaments of communication from the trigeminus, which give it a certain degree of sensibility. The most important of these branches, given off from the inferior maxillary division of the fifth nerve, joins the facial soon after its emergence from the stylomastoid foramen, and thence accompanies its principal ramifications. According to the united testimony of modern experimenters, the facial nerve, if examined on the side of the face, is found sensitive to mechanical irritation, although its sensibility is much inferior to that of the fifth pair. Owing to this communication, the neuralgic pain of tic douloureux sometimes seems to follow the horizontal branches of the facial nerve. The proof, however, that its sensitive fibres are derived from anastomosis and do not originally form part of its trunk, is that the sensibility of the regions to which it is distributed disappears completely after division of the fifth pair, notwithstanding that the facial remains entire.

Beside the communication above mentioned, this nerve contracts frequent anastomoses, in the anterior part of the face, with the supraorbital, infraorbital, and mental branches of the fifth pair.

Communications of the Facial Nerve in the Aqueduct of Fallopius.—While passing through its canal in the petrous portion of the temporal bone, the facial nerve gives off a number of slender filaments by which

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* Leçons sur la Physiologie du Système Nerveux. Paris, 1866, p. 480.

it communicates with other nerves or with ganglia of the sympathetic system. The physiological character of most of these filaments is imperfectly understood; but they are of interest from being usually involved in injury of the nerve within its bony canal, thus producing secondary symptoms, in addition to those of facial paralysis.

FIG. 126.

THE FACIAL NERVE AND ITS CONNECTIONS, within the aqueduct of Fallopius.—1. Fifth nerve, with the Gasserian ganglion. 2. Ophthalmic division of the fifth nerve. 3. Superior maxillary division of the fifth nerve. 4. Lingual nerve. 5. Sphenopalatine ganglion. 6. Otic ganglion. 7. Submaxillary ganglion. 8. Facial nerve in the aqueduct of Fallopius. 9. Great superficial petrosal nerve. 10. Small superficial petrosal nerve. 11. Stapedius branch of facial nerve. 12. Branch of communication with pneumogastric nerve. 13. Branch of communication with glossopharyngeal nerve. 14. Chorda tympani.

At the elbow formed by the anterior bend of the facial nerve, soon after its entrance into the aqueduct of Fallopius, there is a small collection of gray substance, known as the "ganglion geniculatum." From this ganglion a slender filament, the *great superficial petrosal nerve* (Fig. 126, $_9$), runs obliquely forward through the base of the skull, and terminates in the sphenopalatine ganglion ($_5$). This ganglion, which is also connected with the superior maxillary division of the fifth nerve ($_3$), sends branches to the mucous membrane of the posterior part of the nasal passages and the hard and soft palate, and to the levator palati and uvular muscles; that is, to the dilators of the isthmus of the fauces.

This filament of communication between the facial nerve and the sphenopalatine ganglion, is no doubt the motor root of the ganglion, supplying motive force for its muscular branches. Such an inference seems justified by the affection of the palatal muscles accompanying certain cases of facial paralysis from deep-seated lesions. It consists in an incapacity to lift the soft palate, which hangs passively downward, and in a lateral deviation of the uvula, which, according to Longet, is always toward the sound side. The levator palati and uvular muscles being paralyzed, the uvula is drawn into an oblique position toward the non-paralyzed side. As there is no other communication between the facial nerve and the palatal muscles than that through the sphenopalatine ganglion by the great superficial petrosal nerve, the latter must be regarded as containing motor fibres running from the facial to the ganglion.

A little below the last-mentioned filament, the facial nerve gives off a second, the *small superficial petrosal nerve* ($_{10}$), which communicates both with the otic ganglion and with the plexus on the inner wall of the tympanum, known as the "tympanic plexus," which supplies the lining membrane of the tympanic cavity, while the otic ganglion sends a motor filament to the tensor tympani muscle.

From the concave border of the facial nerve, as it bends downward, a fine motor filament, the *stapedius branch* ($_{11}$), passes forward to the stapedius muscle. The facial, therefore, in this part of its course, has an influence on the mechanism of hearing, through the muscles which regulate the tension of the membrana tympani. This influence is exerted directly by its stapedius branch, and indirectly, through the otic ganglion, by the filament supplied to the tensor tympani. Facial paralysis is sometimes accompanied by partial deafness, and sometimes by abnormal sensibility to sonorous impressions; but it has not been determined how far these symptoms are due to paralysis of the muscles of the middle ear, or to the implication of other parts.

From its descending portion, the facial nerve gives off two small branches of communication ($_{12,\,13}$), one to the *pneumogastric* and one to the *glossopharyngeal* nerve, both of which are usually considered as motor filaments. This seems nearly certain in regard to the glossopharyngeal branch; since Cruveilhier describes a separate filament of the facial sometimes passing to the styloglossal and palatoglossal muscles, and Longet cites an instance in which a branch of the facial, on one side, without making connection with the glossopharyngeal nerve, was distributed directly to the palatoglossal and glossopharyngeal muscles; that is, to the constrictors of the isthmus of the fauces.

Finally the facial nerve, shortly before its exit from the stylomastoid foramen, gives off from its concave border the *chorda tympani* ($_{14}$). It first passes in a recurrent direction, traverses the cavity of the tympanum near the inner surface of the membrana tympani, curves downward and forward, and at last joins the descending portion of the lingual nerve. Some of its fibres afterward diverge, passing to the submaxillary ganglion and the submaxillary gland; while others continue onward with the lingual nerve and accompany its distribution in the tongue.

The most positive knowledge in our possession as to the physiological character of the chorda tympani relates to its influence on the phenomena of *circulation and secretion* in the tongue and the submaxillary gland. The experiments of Bernard, corroborated by subsequent observers and especially by Vulpian,* show that galvanization of the chorda tympani increases both the circulation of the blood and the secretion of saliva in the submaxillary gland. But if the chorda tympani be divided both these actions suffer diminution, and the gland remains inexcitable when a sapid substance is introduced into the mouth. If the peripheral extremity of the divided nerve be galvanized, circulation and secretion are excited as before; and the same effect is produced by stimulating, either the lingual nerve, or the filament which

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* Leçons sur l'Appareil Vaso-moteur. Paris, 1875, tome i., p. 150.

it sends to the submaxillary gland. A similar influence is exerted on the circulation in the corresponding half of the tongue; and it is of special importance that this increase of circulatory activity, excited by galvanizing the chorda tympani above its union with the lingual, is also produced, according to Vulpian,* by galvanizing the separated extremity of the divided lingual nerve containing fibres of the chorda tympani. This shows that its influence is in the nature of a motor action; that is, it passes from the central parts toward the periphery, and not in the inverse direction. Finally, while evulsion of the facial nerve from the aqueduct of Fallopius arrests the secretive action of the submaxillary gland, its section at the stylomastoid foramen does not have this effect, but only paralyzes the muscles of the face. This difference depends on the fact that in the former case the chorda tympani is involved in the injury, in the latter it remains intact.

Another symptom observed in deep-seated lesions of the facial nerve, and also dependent on injury of the chorda tympani, is a disturbance of the *sense of taste* in the tip and surface of the tongue. In this affection, the taste is not absolutely abolished, but is diminished in acuteness and in promptitude. If a bitter substance be placed alternately on the two sides of the tongue, it is perceived almost immediately on the sound side, but only after a considerable interval on the side of the paralysis. Various explanations have been suggested for these phenomena, which by most writers are referred exclusively to the chorda tympani. As the fibres of this nerve have so marked an influence on the circulation in the tongue and on salivary secretion, it is plain that when these functions are depressed by its division or injury the sense of taste may be impaired as an indirect result. But whatever be the mechanism of its action, there is no question that its paralysis interferes, to an appreciable degree, with this sense; and an alteration of taste, accompanying facial paralysis on the same side, consequently fixes the location of the nervous lesion at some point within the stylomastoid foramen.

Eighth Pair. The Auditory.

On the posterior surface of the medulla oblongata, a little behind the widest part of the fourth ventricle, a number of white striations run from the neighborhood of the median line transversely outward, toward the peduncles of the cerebellum. These striations represent the roots of the auditory nerve. The nucleus from which they originate is a mass of gray substance beneath them, containing nerve cells of the smaller variety. It extends outward and upward toward the white substance of the cerebellum, with which it is connected by numerous radiating fibres.

From this nucleus the root fibres run almost horizontally outward, and, uniting with each other, curve round the inferior peduncle of the

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* Comptes Rendus de l'Académie des Sciences. Paris, 1879, tome lxxxix., p. 274.

cerebellum to the lateral surface of the medulla at the lower border of the pons Varolii. Some of them follow a deeper course, passing obliquely through the substance of the medulla to the same point. They form the superior or external root of the auditory nerve.

The internal root consists of fibres which, according to Huguenin, may be traced backward from their point of emergence into the inferior peduncle of the cerebellum, where they meet with a second nucleus of gray substance, and continue their course, in company with the longitudinal fibres of the peduncle, toward the white substance of the cerebellum. This connection with the cerebellum is the main anatomical peculiarity by which the auditory is distinguished from the other cranial nerves.

The auditory nerve, formed by the union of these two roots, after emerging from the lateral surface of the medulla oblongata, passes forward and outward, through the internal auditory meatus, and terminates in the nervous expansions of the internal ear.

Physiological Properties of the Auditory Nerve.—The auditory is a nerve of special sense, serving to communicate the impression of sonorous vibrations. In the experiments of Magendie on dogs and rabbits, the auditory nerve, when exposed in the cranial cavity, was found insensible to mechanical irritation, although the roots of the fifth pair exhibited at the same time an acute sensibility. Its exclusive distribution to the internal ear, for which it forms the only nervous connection with the brain, leaves no doubt that its function is that of transmitting to the central organ the nervous influences which produce the sensation of sound.

The remaining cranial nerves, comprising the glossopharyngeal, the pneumogastric, and the spinal accessory, are distributed to the deeper parts about the commencement of the digestive and respiratory passages, where general sensibility is but slightly developed, and the movements are, for the most part, involuntary. Externally, they show a marked similarity of anatomical arrangement, originating one behind the other, in a continuous line, along the lateral furrow of the medulla oblongata and the side of the spinal cord, each by a series of separate filaments; and in such juxtaposition that it is in some instances difficult to say where the root fibres of one terminate, and those of the other begin. The two sensitive nerves belonging to this group, namely, the glossopharyngeal and the pneumogastric, have each a distinct ganglion, situated within their point of emergence from the cranium, and originate from two continuous nuclei at the posterior surface of the medulla oblongata. The motor nerve of the group, or the spinal accessory, originates from a nucleus of its own, and sends branches of communication to the other two. While these nerves, therefore, can hardly be regarded as a single pair, they have nevertheless a close mutual relation both in anatomical arrangement and in physiological properties.

Ninth Pair. The Glossopharyngeal.

The fibres of the glossopharyngeal nerve originate from a nucleus situated a little behind and below that of the auditory, and near the outer border of the fasciculus teres, by which it is separated from the median line. The root-fibres, after leaving the nucleus, pass downward and outward through the medulla, and emerge from its lateral surface, next behind the auditory nerve, in a series of five or six filaments, which soon unite into a single cord. The nerve then passes into and through the jugular foramen, in company with its associated nerves, the pneumogastric and spinal accessory. In this situation it presents a ganglionic enlargement, known as the *petrosal ganglion*, from its occupying a shallow depression in the petrous portion of the temporal bone. It here gives off a small branch, the "nerve of Jacobson," which is distributed to the lining membrane of the tympanum and Eustachian tube, and sends a filament of communication to the otic ganglion of the sympathetic. The trunk of the glossopharyngeal nerve then passes downward and forward, receiving branches of communication from both the facial and the pneumogastric nerves, after which it separates into two main divisions, one of which is destined for the tongue, the other for the pharynx; a double distribution, to which the nerve owes its name. The portion passing to the tongue is distributed to the mucous membrane of the posterior third of this organ, namely, to that portion situated behind the V-shaped row of circumvallate papillæ, and to these papillæ; it also supplies filaments to the tonsils and to the mucous membrane of the pillars of the fauces and the soft palate. The remaining portion of the nerve is distributed to the mucous membrane of the pharynx and to the digastric and stylopharyngeal muscles, by junction with a branch of the facial to the styloglossal muscle, and by junction with branches of the pneumogastric to the superior and middle constrictor muscles of the pharynx. The muscles, accordingly, to which this nerve is directly or indirectly distributed are those by which the tongue is drawn backward (styloglossal), the larynx and pharynx elevated (digastric and stylopharyngeal), and the upper part of the pharynx contracted (superior and middle constrictors); that is, those concerned in the act of deglutition.

Physiological Properties of the Glossopharyngeal.—The glossopharyngeal is for the most part a nerve of sensibility. Its origin from the gray substance in the medulla oblongata corresponding to the posterior horns of the spinal cord, the ganglion located upon its trunk in the jugular foramen, and its principal distribution to the mucous membranes of the tongue and pharynx, all indicate its anatomical resemblance to other sensitive nerves or nerve roots. The result of direct experiment corroborates this view. Longet, in irritating the glossopharyngeal nerve within the cranium, was never able to produce muscular contraction; and although Chauveau, in experimenting upon this nerve in the same situation in recently killed animals, saw its galvanization followed by contraction of the upper part of the pharynx, this effect was probably due to reflex action, since the nerve was still in connection with the medulla oblongata. This conclusion is rendered certain by the investigations of Reid,* who found that irritation of the glossopharyngeal nerve produced movements of the throat and lower part of the face; but these movements were also produced, after the nerve had been divided, by irritation of its cranial extremity. Its sensibility, however, appears to be of a low grade, as compared with that of the trigeminal nerve. While some observers (Reid) found its irritation, outside the jugular foramen, give rise to indications of pain, others (Panizza) have failed to elicit by this means any signs of sensibility whatever; and others still (Longet) speak of them in an uncertain manner. This variation in the observed results is sufficient to show the inferior capacity of the glossopharyngeal nerve for painful impressions; since no experimenter has ever doubted the acute sensibility of the fifth pair.

But notwithstanding the comparative deficiency of this nerve and the parts to which it is distributed, in ordinary sensibility, it serves to transmit impressions of a special character, which are connected with two different but associated functions, namely: 1. The sense of taste, and, 2. The act of deglutition.

Connection with the Sense of Taste.—The sensation of taste exists not only in the anterior portion of the tongue supplied from the lingual branch of the fifth pair, but also at the base of the organ, throughout its posterior third, and in the arches of the palate, supplied by fibres of the glossopharyngeal. But while the region supplied by the fifth pair possesses also a tactile sensibility of high grade, in the posterior region the general sensibility is much inferior to that of taste. The method adopted by Longet for examining the sense of taste in dogs was to place on the base of the tongue a few drops of a concentrated solution of colocynth. Although this always produced, in the natural condition of the animal, manifest signs of disgust, it had no such effect, as a rule, after section of the glossopharyngeal nerves, provided the solution were applied only to the posterior part of the tongue and the pharynx; while if even a minute quantity came in contact with the tip or edges of the organ it caused brisk movements of the jaws with all the indications of repugnance. In the anterior and more movable parts of the tongue, accordingly, the sensations of taste are appreciated, during mastication, by the filaments of the lingual nerve. The glossopharyngeal, on the other hand, is the nerve of taste for the posterior part of the organ; and is called into activity after mastication is accomplished, when the food is carried backward for deglutition and compressed by the base of the tongue, the pillars of the fauces, and the walls of the pharynx.

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* Todd's Cyclopædia of Anatomy and Physiology. Article, *Glossopharyngeal Nerve.*

Connection with Deglutition.—In the fauces and pharynx, the glossopharyngeal nerve is sensitive to certain impressions, which excite the muscles of the neighboring parts and bring into play the mechanism of deglutition. The beginning of this process consists in drawing backward and upward the base of the tongue, by which the masticated food is carried through the isthmus of the fauces into the pharynx. Next, the muscles of the pillars of the fauces (palatoglossal and palatopharyngeal) close the opening of the isthmus, while the soft palate is extended across the upper end of the pharynx, shutting off its communication with the posterior nares; and the constrictor muscles of the pharynx then force its contents downward into the œsophagus. This is an involuntary reflex action. The contraction of the muscles, and their coördination in a series of successive movements, will take place even in a state of unconsciousness under the stimulus of food or liquids in contact with the fauces and pharynx. This contact produces an impression which is conveyed by the glossopharyngeal nerve inward to the medulla oblongata, whence it is reflected in the form of a motor impulse.

Motor Properties of the Glossopharyngeal.—Although this nerve appears to be exclusively sensitive at its origin, it is found, when examined outside the cranium, to possess motor properties. In the experiments of Mayo on the ass, confirmed by those of Longet on the horse and dog, irritation of the glossopharyngeal nerve in the neck produced contraction of the stylopharyngeal muscle and the upper part of the pharynx. These movements were the result of direct motor action, since, in the experiments of Longet, they were excited by irritating the peripheral extremity of the divided nerve.

The glossopharyngeal, therefore, after its exit from the jugular foramen, is a mixed nerve. In addition to its original sensitive filaments, it has received a branch of communication from the facial, and also a branch from the pneumogastric. The latter branch is regarded, on anatomical grounds, as made up, wholly or in part, of motor fibres coming from the spinal accessory, through its anastomosis with the pneumogastric. The results obtained by experiment also indicate a double source for the motor fibres of the glossopharyngeal nerve. If these were derived exclusively from either the facial or the spinal accessory, the division of one or the other of these nerves above its communicating branch would abolish completely the motor power of the glossopharyngeal. But the experiments of Bernard and Longet, in which the facial nerve was divided in the aqueduct of Fallopius, and those in which the spinal accessory was destroyed on both sides, show that the process of deglutition, though retarded, is not abolished by either operation.

Beside these anastomotic branches near its origin, the glossopharyngeal is joined by a second branch from the facial, which accompanies it to the styloglossal muscle, and perhaps also to the pillars of the fauces; and, according to Cruveilhier, a branch derived from the spinal accessory takes part in the formation of the pharyngeal plexus supplying the upper constrictor muscles of the pharynx. The process of deglutition, therefore, is excited at its commencement by sensitive impressions conveyed through the glossopharyngeal nerve; but its movements are executed by a reflex impulse transmitted through the motor fibres of several distinct branches of communication.

Tenth Pair. The Pneumogastric.

The pneumogastric nerve, remarkable for its extensive course and varied distribution, has received its name from the two most important organs in which it terminates, namely, the lungs and stomach. It arises from the side of the medulla oblongata by ten or fifteen filaments, arranged in linear series continuously with those of the glossopharyngeal. Their nucleus of origin is an extended tract of gray substance on the posterior surface of the medulla oblongata, just outside the lower extremity of the fasciculus teres. This deposit, which, by the divergence of the posterior columns, is exposed to view on the floor of the fourth ventricle, is known as the *ala cinerea*. At its anterior extremity it is continuous with the nucleus of the glossopharyngeal; and at its posterior extremity it joins that of the spinal accessory. From its deep surface it gives out the root fibres of the pneumogastric nerve, which run downward and outward through the medulla, and emerge, in the above mentioned series of filaments, from its lateral surface.

The filaments of the pneumogastric, after leaving the medulla, unite into a trunk which passes out of the cranium by the jugular foramen. Here it presents a ganglionic swelling, known as the "jugular ganglion." At or immediately beyond this situation, the nerve is joined by a motor branch from the spinal accessory; and it afterward receives similar filaments from four other sources; namely, the facial, the hypoglossal, and the anterior branches of the first and second cervical nerves.

While passing down the neck the pneumogastric nerve contributes an anastomotic branch to the pharyngeal plexus. Its first important branch of distribution is the *superior laryngeal nerve*, which penetrates the larynx by an opening in the thyro-hyoid membrane, and is distributed to the mucous membrane of the epiglottis and the laryngeal cavity. It also gives off a small muscular branch to the inferior constrictor of the pharynx and to the crico-thyroid muscle of the larynx. It supplies several filaments, which, with others from the great sympathetic, form the *laryngeal plexus;* and by this plexus it sends fibres to the upper cardiac nerves of the sympathetic. Other filaments which it gives off in the neck also join the cardiac branches of the sympathetic, or sometimes, according to Cruveilhier, pass directly to the cardiac plexus beneath the arch of the aorta.

The next branch is the *inferior laryngeal nerve*, which separates from the pneumogastric after its entrance into the chest, and ascends, between the trachea and œsophagus, to the larynx, giving off filaments to the œsophagus and the inferior constrictor of the pharynx. This nerve is distributed to all the muscles of the larynx, except the crico-thyroid already supplied by the superior laryngeal. The larynx therefore receives from the pneumogastric two different branches, of distinct properties and functions. The superior laryngeal branch is mainly a sensitive nerve, supplying the mucous membrane; the inferior laryngeal branch is motor, and provides for the activity of the laryngeal muscles.

The most important dependency of the pneumogastric nerve in the chest is the *pulmonary plexus.* This is formed by a number of inosculating branches, from which the filaments of distribution pass, along the bronchi and their subdivisions, to the pulmonary lobules. In the inferior portion of the chest, other inosculating branches surround the œsophagus with the *œsophageal plexus*, from which fibres are supplied to its mucous membrane and muscular coat.

The pneumogastric nerves, after reunion of their branches below the pulmonary plexus, enter the abdomen and spread out in two sets of *gastric branches*, which supply the mucous membrane and muscular coat of the stomach. Those from the left pneumogastric nerve supply the anterior wall of the organ, and send filaments to the transverse fissure of the *liver*, into which they penetrate in company with the hepatic plexus of the sympathetic; those from the right pneumogastric supply the posterior wall of the stomach, and finally communicate with the solar plexus of the sympathetic.

FIG. 127.

ORIGIN AND CONNECTIONS OF THE GLOSSOPHARYNGEAL, PNEUMOGASTRIC, AND SPINAL ACCESSORY NERVES.—1. Facial nerve. 2. Glossopharyngeal. 3. Pneumogastric. 4. Spinal accessory. 5. Hypoglossal. 6. External (muscular) branch of the spinal accessory. 7. Superior laryngeal branch of the pneumogastric. 8. Pharyngeal plexus. 9. Laryngeal plexus and upper cardiac branches of the pneumogastric. 10. Tympanic plexus, from a branch of the glossopharyngeal. (Hirschfeld.)

The pneumogastric nerve, therefore, is distributed to the passages by which air and food are introduced into the body. It also forms connection at several points with the great sympathetic, and, through it, sends fibres to the heart.

Physiological Properties of the Pneumogastric.—According to Longet, the pneumogastric at its origin is exclusively sensitive. Irritation of the nerve roots, separated from the medulla, is without effect; but if applied to the trunk of the nerve at a lower level, it excites muscular contraction. At this situation the nerve contains motor fibres derived from the spinal accessory, the facial, the hypoglossal, and the two upper cervical nerves. It is, accordingly, a mixed nerve, and is capable of providing both for movement and sensibility in the organs to which it is distributed.

Its sensibility, however, to mechanical irritation is but slightly marked, as shown by the experience of all observers. It may frequently be divided, in the unetherized animal, without causing signs of pain; and this want of reaction is at times so complete as to indicate entire absence of ordinary sensibility. In other instances, according to Bernard, it appears sensitive; but the conditions on which this difference depends are unknown. It is certain that, as a rule, the pneumogastric is deficient in that kind of sensibility which produces pain; and the organs to which it is distributed have little or no appreciation of tactile impressions. Nevertheless, it evidently possesses a sensibility of peculiar kind, and of the highest importance for the vital functions.

Connection with Respiration.—The most important endowment of the pneumogastric nerve is that connected with the movements of respiration. Its influence in this respect is evident from the results following its division in the neck.

When the nerves have been simultaneously divided on both sides in the dog, and the slight disturbance which immediately follows their section has subsided, the most striking change produced in the animal's condition is a *diminished frequency of respiration.* The respiratory movements sometimes fall at once to ten or fifteen per minute, becoming, in an hour or two, still more infrequent. They are performed easily and regularly; and the animal, if undisturbed, usually remains quiescent, without any special sign of discomfort. By the second or third day the respirations are often reduced to five, four, or even three per minute; the general condition of the animal being also exceedingly sluggish. The movement of inspiration is slow, easy, and silent, occupying several seconds in its duration; while that of expiration is sudden and audible, and is accompanied by a well-marked effort, which has, to some extent, a convulsive character. The intercostal spaces sink inward during the lifting of the ribs; and the whole movement of respiration has an appearance of insufficiency, as if the lungs were not thoroughly filled with air.

Death takes place from one to six days after the operation; the only marked symptoms during this time being steady failure of the respiration, with increasing general sluggishness. After death the lungs are found in a peculiar state of solidification; of a dark purple color, leathery and resisting to the touch, destitute of crepitation, and infiltrated with blood. Pieces of the pulmonary tissue cut out sink in water. The pleural surfaces, however, are natural in appearance, and there is no effusion into the pleural cavity. The lungs are simply engorged with blood, and, to a considerable extent, empty of air.

The inference from these phenomena is that the pneumogastric nerves are the channels for a sensitive impression from the lungs to the medulla oblongata which excites, by reflex action, the movement of respiration. Consequently when they are divided, their impression being no longer conveyed to the nervous centres, the reflex act in the medulla lacks its usual stimulus, and the movements of respiration diminish in frequency. They do not cease altogether, because a similar impression comes from other parts of the circulatory system. But the lungs are the organs most directly concerned in respiration, and the most sensitive to its deficiency; and when their influence is cut off, the greater part of the normal respiratory stimulus is wanting. The medulla, accordingly, reacts less frequently, and the movements of respiration are performed at longer intervals.

This appears to be the only explanation which will account for the immediate effects of dividing the pneumogastric nerves. The infrequency of respiration which follows directly upon this operation is not due to paralysis of the respiratory muscles. It is not accompanied by dyspnœa, nor by any sign of distress from defective respiration. It is evident that the animal does not feel the need of breathing as under ordinary conditions, and consequently makes no effort to compensate for the loss. If respiration were reduced in frequency, the pneumogastric nerves remaining entire, a sense of suffocation would soon be manifest. This happens when the breath is voluntarily suspended; the sensation of discomfort being first perceptible in the lungs, but afterward extending over the whole system, and assuming the character of an intolerable distress. When breathing is renewed, the unpleasant sensation disappears, as inspiration renovates the air in the pulmonary cavities. The impression transmitted by the pneumogastric nerves to the medulla is sufficient to maintain respiration at its normal frequency. When this impression is cut off, the rate of respiration is lowered nearly one-half.

But the subsequent changes after this operation are due to other causes. When the pneumogastric nerves are divided in the middle of the neck, the fibres of the inferior laryngeal nerve are involved in the section. This paralyzes the laryngeal muscles, including those which separate the vocal chords and open the glottis at the moment of inspiration (page 238). The glottis is then left in a condition of flaccidity, and instead of opening in inspiration for the admission of air, it collapses and obstructs the passage. The quantity of air entering the lungs is thus diminished, and the aeration of the blood still further impaired. This no doubt causes the general sluggish condition of the nervous system after section of the pneumogastrics. The medulla participates in this derangement. It becomes less sensitive to the respiratory stimulus; and as the stimulus itself is diminished, these conditions react upon each other, and increase the difficulty of respiration. Thus the breathing becomes slower and slower, until it is at last so infrequent that it can no longer sustain life.

Furthermore, the physical change in the pulmonary tissues is superadded to their functional derangement. This alteration has no inflammatory character, but consists in a diminution of the air in the vesicles of the lungs, and a passive accumulation of blood in the capillaries. It combines with the causes already described, to interfere with the aeration of the blood and to hasten the failure of the vital powers.

Protection of the Glottis from Foreign Substances.—The superior laryngeal branch of the pneumogastric supplies to the mucous membrane of the larynx a peculiar sensibility which is essential for the protection of the respiratory passages. It stands as a sort of sentinel, at the entrance of the glottis, to prevent the intrusion of foreign substances. If a crumb of bread fall within the aryteno-epiglottidean folds, or on the edges of the vocal chords, the sensibility of the parts excites an expulsive cough, by which the foreign body is dislodged. The impression conveyed inward by the superior laryngeal nerve is reflected upon the expiratory muscles of the chest and abdomen, by which the movement of coughing is accomplished. This reaction is dependent on the sensibility of the laryngeal mucous membrane; and it can no longer be produced after section of the superior laryngeal nerve.

Connection with the Voice.—In addition to its function in respiration, the larynx is an organ for the production of vocal sounds. The formation of the voice can be studied in animals after exposing the glottis by the operation of pharyngotomy; and in man by the use of the laryngoscope. The first important fact demonstrated in this way is that the voice is formed always in expiration, never in inspiration. The column of outgoing air is set in vibration by the glottis, and its resonance modified in the pharynx, mouth, and nasal passages. Secondly, it requires tension and approximation of the vocal chords, by which the orifice of the glottis is narrowed to a comparatively minute crevice. When the vocal chords are relaxed during expiration, nothing can be heard except a faint whisper of the air passing through the larynx. In the production of a vocal sound the chords are made tense and closely applied to each other; and the air, driven by forcible expiration through the narrowed chink of the glottis, between the vibrating vocal chords, is itself thrown into sonorous vibration. The tone, pitch, and intensity of the sound vary with the conformation of the larynx, the tension and approximation of the vocal chords, and the force of expiration. The narrower the opening and the greater the tension of the chords, the more acute the sound; while a wider opening and a lower tension produce a graver note. The quality of the sound is also modified by the length of the column of air between the glottis and the mouth, the tense or relaxed condition of the pharynx and fauces, and the dryness or moisture of the mucous membrane.

The production of a vocal sound takes place, therefore, in the larynx;

while articulation, or division of the sound into vowels and consonants, words and phrases, is accomplished by the lips, tongue, teeth, and palate. Consequently, division of the pneumogastric nerve or of its inferior laryngeal branch on both sides, produces loss of voice. Furthermore, as vocalization and articulation are distinct nervous actions, they may be deranged independently of each other, by injury or disease of different parts of the nervous system. The movements of articulation are regulated by the facial and hypoglossal nerves; while vocalization is under the control of the pneumogastric.

Connection with Deglutition.—The act of deglutition, which commences in the fauces and pharynx, is continued and completed by the lower portion of the pharynx and by the œsophagus. These parts receive both their sensitive and motor filaments from the pneumogastric nerve, and under its influence the food, once started on its downward passage, is conducted by the peristaltic action of the œsophagus into the stomach.

The inferior constrictor of the pharynx and the cervical portion of the œsophagus both receive filaments from the inferior laryngeal nerve; while the thoracic portion of the œsophagus is supplied from the trunk of the pneumogastric. Deglutition, therefore, becomes incomplete, as shown by Bernard in dogs, horses, and rabbits, by division of the pneumogastric nerves in the neck. The masticated food is still conveyed by the pharynx from the fauces to the œsophagus; but here it accumulates, distending the walls of the paralyzed canal, and finding its way into the stomach only in small quantities under the pressure from above. The normal process of swallowing is accomplished by a series of contractions, beginning at the fauces and ending at the stomach. Each portion of the mucous membrane receives in turn a stimulus from the contact of the food, followed by excitement of the corresponding muscle; so that the alimentary mass is carried rapidly downward by reflex action, independent of voluntary control. Section of the pneumogastric nerves destroys sensibility and motive power in the œsophagus, and consequently interferes with deglutition.

Protection of the Glottis in Deglutition.—As the laryngeal orifice communicates directly with the cavity of the pharynx, and as all solids and liquids, in swallowing, pass over its surface, portions of the food would find their way into the larynx unless there were some means for its protection. The epiglottis, which stands in front of the glottis, and shuts over it like a cover when the tongue is drawn back in deglutition, might seem to be a safeguard in this respect.

But experience shows that this organ is not essential to protect the glottis in deglutition. It may be completely excised, in dogs, without any subsequent difficulty in swallowing either liquid or solid food. The epiglottis, furthermore, exists only in mammalians, being absent in all other vertebrate animals. Finally, the epiglottis does not prevent foreign substances passing into the larynx when the other conditions of normal deglutition are disturbed. The protection of the glottis against the entrance of food does not depend on a mechanical obstacle, but on a special association of nervous acts.

The first requisite for swallowing is the *suspension of respiration.* This takes place, at the beginning of deglutition, by an influence designated as the "action of arrest." The same nervous impression which excites contraction of the pharynx, suspends for a time the movement of inspiration.

The effect of this arrest is to prevent the opening of the glottis. As the respiratory movements of the glottis are coincident with those of the chest, and are excited by the same nervous influence, the impression which puts a stop to one also suspends the other. The glottis consequently not being opened when food enters the pharynx, its liability to admit any portion of the alimentary mass is considerably diminished. But it is furthermore completely closed by the inferior constrictor of the pharynx, the most active muscle in the apparatus of deglutition; since the fibres of this muscle are attached to the external surface and borders of the thyroid cartilage, thus compressing the larynx on both sides at the instant of deglutition. By this means the glottis is protected, as in birds and reptiles, even where an epiglottis is wanting.

The accident by which food or foreign substances sometimes gain access to the larynx, in man, is always caused by a sudden attempt at inspiration. This cannot take place during deglutition in the ordinary state of the nervous system; but it may be produced by any unexpected shock or excitement which disturbs the coördination of the reflex actions. Such a shock usually causes, as its first effect, a spasmodic inspiration; and if this take place while food is passing through the pharynx, a portion of it finds its way through the open orifice of the glottis into the larynx.

Connection with Stomach Digestion.—The effect produced on the stomach by division of the pneumogastric nerve shows that its influence on this organ is mainly similar to that which it exerts on the œsophagus; that is, it supplies the mucous membrane with a special sensibility to the contact of food, and provides for the peristaltic action of the muscular coat. After section of both pneumogastric nerves in the neck, the sensations of hunger and thirst remain; the animals often exhibiting a desire for food and drink, which they sometimes take in considerable quantity, though but little reaches the stomach, owing to the paralysis of the œsophagus. In the experiments of Bernard on dogs, the secretion of gastric juice was suspended after this operation, and food introduced into the stomach through a gastric fistula remained undigested. But Longet found that if the food were introduced only in small quantity, it might cause the secretion of gastric juice, and be finally digested. This indicates that secretion and digestion in the stomach are not immediately under the control of the pneumogastric nerve, but that after its section they become practically suspended, owing mainly to paralysis of the muscular coat.

According to Bernard, the finger, if introduced into the stomach through a gastric fistula in a healthy dog, is compressed with considerable force by the walls of the organ; but this pressure disappears completely on division of the pneumogastric nerves. The absence of muscular action in a paralyzed stomach is sufficient to account for the failure of digestion. This action is necessary to bring successive portions of the food in contact with the mucous membrane, and for the thorough admixture of gastric juice with the alimentary mass. The pneumogastric nerves therefore supply to the stomach a sensibility and motor power, which are practically essential to the digestive process.

Influence on the Heart.—The pneumogastric filaments, destined for distribution in the heart, are partly derived from its superior laryngeal branch, whence they join the upper cardiac nerve coming from the superior cervical ganglion of the sympathetic. Others are furnished by the trunk of the pneumogastric in the neck, which inosculates with the continuation of the upper cardiac nerve. The inferior laryngeal branch, during its reascending course, supplies so many filaments to the same plexus that, according to Cruveilhier, it sometimes appears distributed in almost equal proportions to the larynx and to the heart. Finally other small branches of the pneumogastric in the chest lose themselves at once in the cardiac plexus, beneath the arch of the aorta. All the filaments, accordingly, finally reaching the heart through the cardiac plexus, originate either from the sympathetic or the pneumogastric; and the entire group is characterized by the frequent and intimate admixture of fibres from these two sources.

The effect produced on the heart by irritation of the pneumogastric is precisely the opposite to that usually caused by irritating the nerves of a muscular organ. If the heart be exposed in a warm-blooded quadruped by opening the chest, and the circulation maintained by artificial respiration, the action of the pneumogastric may be studied by applying to its trunk the poles of a galvano-faradic apparatus. On stimulating the nerve in this way with an interrupted current of moderate strength, the first visible effect is a *diminution in frequency of the cardiac pulsations.* If the intensity of the current be increased, the heart acts still more slowly; and with a further increase of intensity it stops altogether.

When the faradization of the nerve is suspended, the cardiac pulsations recommence; and this may be repeated for many successive trials.

There are three important facts to be noted in regard to these phenomena:

I. When the heart ceases to move, under the faradization of the nerve, it stops in the condition of muscular relaxation. It lies flaccid and motionless, while its cavities are slowly filled with blood returning from the venous system. On stopping the faradization, on the other hand, the first sign of activity in the heart is a normal pulsation. Stimulation of the pneumogastric nerve, accordingly, tends to arrest the muscular action of the heart.

II. If the pneumogastric nerve be divided, and the faradic current applied to its central extremity, the heart's pulsations are not interrupted; but when the current is applied to the peripheral extremity of the nerve, they cease as before. The influence therefore which arrests the heart's action, under stimulation of the pneumogastric, is not a centripetal influence, operating through the nervous centres; it is a centrifugal influence, passing from above downward through the pneumogastric to the heart.

III. After stimulating the pneumogastric nerve with a current sufficient to stop the cardiac pulsations, if the current be continued the heart does not remain motionless. At the end of ten or fifteen seconds it performs a beat. A little later this is repeated, and the pulsations then recur, with increasing frequency, until their normal rate is reëstablished, notwithstanding the continued faradization of the nerve. This shows that the nervous action which arrests the heart is exhausted after a certain time. If the stimulation be now applied to the pneumogastric nerve of the opposite side, the heart stops, as before. The heart, accordingly, is still sensitive to the action of arrest; it is the nerve only which, by continued excitement, loses the power of exerting this action. But after a pneumogastric nerve has been thus exhausted, so that it no longer retards the cardiac pulsations, if allowed to repose for a time, and again stimulated, it again stops the heart; showing that it has recovered the power which it had temporarily lost. In these respects, the influence of the pneumogastric nerve on the heart resembles that of a motor nerve on the muscles of the limbs. The difference between the two is in their effect. An ordinary motor nerve, when stimulated, causes contraction of the corresponding muscle; stimulation of the pneumogastric nerve, as connected with the heart, causes relaxation.

Eleventh Pair. The Spinal Accessory.

This nerve, so named from its spinal origin and subsequent association with the cranial nerves, consists of filaments emerging from the cervical portion or the spinal cord, from the level of the fourth or fifth cervical nerve upward (Fig. 127, $_4$). They unite into a slender cord, which ascends between the anterior and posterior roots of the cervical spinal nerves, to the foramen magnum, where it enters the cranial cavity. Here it receives a new supply of root fibres from the medulla oblongata, arranged in a continuous line with those of the pneumogastric. The nerve trunk, thus constituted by the union of its spinal and medullary roots, accompanies the pneumogastric and glossopharyngeal nerves in their passage through the jugular foramen.

The central origin of this nerve is a collection of nerve cells situated in the upper portion of the spinal cord and the medulla oblongata, on the outer and posterior aspect of the anterior horn of gray substance. From this source its fibres curve downward and outward to their point of emergence on the lateral surface of the medulla.

While passing through the jugular foramen, the spinal accessory becomes adherent to the jugular ganglion of the pneumogastric, but without taking part in its formation, except by furnishing one or two small filaments of communication. Immediately after its exit from the foramen it divides into two main branches; namely, 1st, the *internal*, or anastomotic branch, which joins the trunk of the pneumogastric, and 2dly, the *external*, or muscular branch, which passes downward and outward and is distributed to the sterno-mastoid and trapezius muscles. According to many observers (Bernard, Cruveilhier, Henle, Longet) the internal or anastomotic branch is made up of fibres from the medulla oblongata; the external or muscular branch consists of those originating from the spinal cord.

The spinal accessory is without question a motor nerve. According to Bernard and Longet, mechanical or galvanic irritation applied, within the cranium, to the central extremity of the divided nerve, causes no indication of sensibility. On the other hand its fibres may be traced in great part directly to their termination in muscular tissues, and its division or evulsion induces effects which consist exclusively in the loss of motive power.

The most complete method of experimenting on this nerve is that adopted by Bernard, namely, its evulsion. For this purpose, the muscular branch of the nerve is followed by dissection to its point of emergence from the jugular canal, where it separates from the anastomotic branch. The combined trunk is then seized between the blades of a forceps, and by steady and continuous traction the whole nerve, with its medullary and spinal roots, may be extracted entire. By appropriate variations of the procedure, either the medullary portion with the anastomatic branch, or the cervical portion with the external branch, may be removed separately, and the comparative effects of the two operations observed. But when the whole trunk is extracted as above, all its fibres, both anastomotic and muscular, are destroyed at the same time.

The most striking effects of this operation are those due to paralysis of the internal or anastomotic branch. From this branch the pneumogastric nerve receives a large share of its motor fibres. According to Cruveilhier, the pharyngeal filament is sometimes given off exclusively from the anastomotic branch of the spinal accessory, sometimes partly from this branch and partly from the pneumogastric. Beyond this point, the fibres of the pneumogastric nerve derived from the spinal accessory can no longer be followed by dissection; but the results of experiment show that they are finally distributed, through the inferior laryngeal branch, to the muscles of the larynx, where they preside over its action as a vocal organ.

After evulsion of the spinal accessory nerve on both sides, the most noticeable result is *loss of power to produce vocal sounds.* The respiratory movements of the glottis are not interfered with; but the voice is completely lost, as much so as if the inferior laryngeal nerves, or the pneumogastric trunks themselves, had been divided. The total result in the two cases, however, is very different. Section of the pneumogastrics, or of their inferior laryngeal branches, paralyzes all the movements of the glottis, those of respiration as well as those of phonation; since these nerves contain all the motor fibres distributed to the larynx, except those for the crico-thyroid muscles. On the other hand, evulsion of the spinal accessory nerves paralyzes the movements of phonation alone, namely, those in which the vocal chords are approximated and the rima glottidis narrowed; leaving untouched the movements of respiration, in which the vocal chords are separated and the glottis opened.

The larynx, accordingly, performs two distinct functions, and is supplied with motor nerves from two different sources. Those which preside over the production of sound originate from the spinal accessory; those for respiration are derived from other motor nerves (facial, hypoglossal, cervical) which also communicate with the pneumogastrics.

The function of the *external* or muscular branch of the spinal accessory nerve is not so fully understood. The sternomastoid and trapezius muscles, to which it is distributed, also receive filaments from the cervical spinal nerves; and they still retain the power of motion after evulsion of the spinal accessory on both sides. The sternomastoid and trapezius muscles have no such peculiar action as that of the larynx in vocalization; and it is not easy to distinguish what movements of these muscles are paralyzed by division of the spinal accessory, and what remain unaffected. The most plausible conclusions are those derived by Bernard from the continued observation of animals after division of these nerves.

According to this view, the external branch of the spinal accessory, like the internal branch, performs a function antagonistic to respiration. Respiration is naturally suspended during strenuous and prolonged muscular effort. In the acts of straining, lifting, pushing, and the like, respiration ceases, the spinal column is made rigid, and the head and neck are fixed in position largely by means of the sternomastoid and trapezius muscles. Such efforts cannot be made with success if these muscles be paralyzed. According to Bernard, they also take part in the production of a cry, or prolonged vocal sound. After destruction of the entire spinal accessory the voice is completely abolished by paralysis of the laryngeal muscles. If its external branch alone be divided, the animal can still produce a vocal sound; but this sound cannot be prolonged into a cry, and the voice is confined in duration to the ordinary length of an expiratory movement. Although the animals, furthermore, are apparently not otherwise inconvenienced by this operation so long as they remain quiet, any increased exertion, as in running or leaping, causes a want of harmony between respiration and muscular action, which results in shortness of breath.

The sternomastoid and trapezius muscles, like those of the larynx, are therefore animated by two sets of motor fibres. Those coming from the cervical spinal nerves provide for the ordinary movements of locomotion; those derived from the spinal accessory supply the stimulus for continuous muscular exertion, or for a prolonged vocal sound.

Twelfth Pair. The Hypoglossal.

The hypoglossal nerve, or the motor nerve of the tongue, emerges from the anterior part of the medulla oblongata by ten or twelve slender filaments between the anterior pyramids and the olivary bodies (Fig. 127, $_5$), on a line with the anterior roots of the cervical spinal nerves.

The central origin of these fibres, according to Clarke, Dean, Kölliker, Henle, and Meynert, is a nucleus of gray substance in the posterior part of the medulla oblongata next the median line, at the inferior extremity of the fourth ventricle. It has an elongated form, extending from the divergence of the posterior columns upward and forward to the level of the auditory nucleus. It is parallel in position with the spinal accessory and pneumogastric nuclei, but situated between them and the median line.

During the passage of the hypoglossal nerve roots through the medulla oblongata, they reach the inner surface of the olivary nucleus, and pass in great measure between the folds or through the substance of its convoluted wall. It is shown by Dean* that although a direct continuity between the root fibres of the nerve and the cells of the olivary nucleus cannot be demonstrated, yet prolongations of these cells can sometimes be traced upward and inward, in company with the nerve roots, toward the hypoglossal nucleus; and in the sheep, the tracts of fibres connecting the two nuclei are very evident. According to Henle, in some transverse sections through the olivary body fibres from the hypoglossal nerve roots may be seen bending round the inner border of the nucleus into its interior; while others emerge in a corresponding manner from the opposite border and continue onward, with the main root-bundles, to the hypoglossal nucleus. Although the minute anatomical structure of these parts is not fully made out, it is evident that a close relation exists between the gray substance of the olivary bodies and the hypoglossal nucleus and roots.

Kölliker regards the roots of the hypoglossal nerves as undergoing complete decussation through the raphe, at the level of the nuclei. According to Clarke and Dean, a portion of the fibres of each root terminate in the corresponding nucleus, while another portion decussate with those of the opposite side. It is certain that the hypoglossal, like other cranial nerves, has, in some way, a connection with the opposite side of the brain; since cases of facial paralysis from cerebral hemorrhage are often accompanied by paralysis of the tongue on the same side with that of the face, and opposite to the lesion. One of the genio-

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* Gray Substance of the Medulla Oblongata and Trapezium. Washington, 1864, p. 36.

hyoglossal muscles having lost its power, while the other remains active, the point of the tongue, when protruded, deviates toward the paralyzed side.

After leaving the medulla oblongata, the fibres of the hypoglossal nerve become parallel with each other, and, passing through the anterior condyloid foramen, emerge from the skull in the form of a cylindrical cord. Immediately beyond this point it presents one or two branches of communication with the pneumogastric, where it crosses the track of this nerve. According to Cruveilhier, these branches consist of fibres from the hypoglossal nerve which join those of the pneumogastric, and run with them in a peripheral direction. The hypoglossal nerve then passes downward, nearly to the level of the hyoid bone, where it curves forward, giving filaments to the styloglossal and hyoglossal muscles, and to those immediately beneath the hyoid bone; after which it turns upward, penetrating the tongue from below, inosculates with the lingual branch of the fifth pair, and is finally distributed to the muscles of the tongue. It, therefore, animates not only the lingual muscles proper, but also those which draw the tongue backward and upward (styloglossal), and backward and downward (hyoglossal and infrahyoid muscles). It also receives filaments from the first and second cervical nerves, which, according to Cruveilhier, are fibres of reinforcement, accompanying the hypoglossal nerve to its peripheral termination.

Physiological Properties of the Hypoglossal Nerve.—The motor character of this nerve is easily established by the results of its irritation and division. If it be exposed, either in the living or the recently-killed animal, where it runs parallel to and a little above the hyoid bone, its irritation produces immediate convulsive action of the tongue. The same effect follows irritation applied to the peripheral extremity of the divided nerve; showing that the contractions thus produced are not reflex, but due to a direct stimulus conveyed through the nerve to the tongue. Whether the nerve possess also sensitive fibres of its own is not certain. Longet obtained in this respect only negative results; the division of the nerve roots in dogs, between the occiput and the atlas, not producing perceptible signs of pain. Outside the cranial cavity, according to nearly all experimenters, it possesses some degree of sensibility; but this is probably derived, by inosculation, from the first and second cervical nerves near the base of the skull, and from branches of the fifth pair near its terminal distribution. Whatever sensibility it may possess is destined only for the muscular substance of the tongue, and not for its mucous membrane; since division of the lingual branch of the fifth pair and of the glossopharyngeal nerve destroys sensibility over the whole surface of the organ, though the hypoglossal be untouched; and secondly, the tongue evinces its ordinary sensibility, according to Longet, after the division of both hypoglossal nerves.

The uniform result of section of both hypoglossal nerves is loss of muscular power in the tongue, while its tactile and gustatory sensibilities are preserved. In the experiments of Panizza and Longet, the animals after this operation were unable to move the tongue in any direction; and in mastication it was liable to be caught and wounded by the teeth. It was therefore reduced to a helpless condition, by division of its motor nerves.

Connection with Mastication and Deglutition.—Although the movements of the tongue take no direct part in mastication, they are yet essential to its performance, by bringing successive portions of the food between the teeth and removing those which have undergone trituration. In animals which introduce liquids into the mouth by lapping, this act also becomes impossible after section of the hypoglossal nerves. The action of the lingual muscles is practically of so much importance that, according to Longet, it requires great expenditure of time and patience, in keeping animals with paralysis of the tongue, to supply them with sufficient nourishment for the support of life.

Connection with Articulation.—In man, another function performed by the tongue is that of articulation. As the lingual muscles are important for the pronunciation of all consonants except the labials (*b*, *m*, *p*) and the labio-dentals (*f*, *v*), as well as for that of the vowels, *a*, *e*, *i*, and *y*, their paralysis produces a nearly complete incapacity of articulation. In man, disease or injury of the hypoglossal nerve alone is a rare occurrence, and, when it exists, is almost invariably confined to one side. In glosso-labio-laryngeal paralysis, from lesion of the medulla oblongata (p. 445), the disease is of central origin, and affects other muscles as well as those of the tongue. In these cases, however, the imperfect action of the lingual muscles is an early sign; and when the disease is fully developed and the tongue completely paralyzed, all power of articulation is lost.

The hypoglossal nerve, accordingly, though one of the simplest of the cranial nerves in its physiological endowments, is important as an aid in mastication and deglutition, and essential for the production of articulate speech.

CHAPTER VII.

THE SYMPATHETIC SYSTEM.

THE sympathetic nerves, as compared with those of the cerebro-spinal system, have certain peculiarities of arrangement and distribution. The double nervous cord running through the great cavities of the body, the numerous and scattered ganglia, united with each other by slender filaments, the frequent plexiform arrangement of the branches, and their distribution to the organs of circulation and nutrition, form a well-marked group of anatomical features. But notwithstanding the general importance of these characters, the sympathetic nerves and ganglia do not constitute an independent nervous system. Neither their anatomical elements nor their external connections are essentially different from those of the cerebro-spinal nerves and centres. The sympathetic trunks and branches contain medullated nerve fibres like those of the spinal nerves; and its ganglia contain nerve cells with prolongations in the form of axis cylinders. The main peculiarity of the sympathetic nerve fibres is that they are, as a rule, of small diameter, though not smaller than the average of those in the cerebro-spinal nerves. The cells of the sympathetic are also generally small, never, according to Kölliker, equalling the largest of those in the spinal cord or the brain; and they are also characterized by the frequency with which they send out a single prolongation, becoming apparently the source of new fibres.

On the other hand, the posterior roots of the spinal nerves are provided with ganglia similar to those of the sympathetic system. The same arrangement exists in some of the cranial nerves, as in the pneumogastric, glossopharyngeal, and the fifth pair. Thus all the sensitive and mixed cerebro-spinal nerves contain fibres of ganglionic origin, in addition to those from the brain and spinal cord. Furthermore, all the sympathetic ganglia receive filaments from the cerebro-spinal nerves, the fibres of which, there is reason to believe, pass through the ganglion to the peripheral branches of the sympathetic system. This is inferred from the fact that many of these fibres cannot be seen either to originate or terminate in the ganglion, and also from the paralyzing effect produced on a muscular organ supplied with sympathetic fibres, by division of the cerebro-spinal nerve which communicates with its ganglion. This is especially shown by dilatation of the pupil following division of the oculomotorius nerve, which supplies the iris with a motor branch through the ophthalmic ganglion. The numerous filaments supplied by the pneumogastric nerve to the cardiac branches of the sympathetic, and to the cardiac plexus, afford a striking instance of the same kind.

The ganglia on the spinal and cranial nerve roots are undoubtedly analogous, in their anatomical relations, to those of the sympathetic system; and this system may be considered as made up of nervous centres disseminated through the great cavities of the body, and connecting filaments which receive fibres from the cerebro-spinal nerves and supply to these nerves fibres of their own. All the organs in the body, accordingly, contain nerve fibres from both sources; the difference consisting in the relative numbers of one kind or the other in particular parts. The cerebro-spinal nerves are in greatest abundance, and manifest their most striking properties, in the organs of animal life; those of the sympathetic system preponderate in the organs of nutrition, and in their influence on the functions of circulation, secretion, and growth.

General Arrangement of the Sympathetic System.—The central part of the sympathetic system is a double chain of ganglia, on the sides of the spinal column, united with each other by longitudinal filaments. Each ganglion is connected, by motor and sensitive fibres, with the cerebro-spinal system. Its nerves are distributed to glands and mucous membranes, mostly destitute of general sensibility, and to muscular fibres which are independent of the will. The sympathetic ganglia are situated in the head, neck, chest, and abdomen; and in each of these regions are connected by their nerves of distribution with special organs.

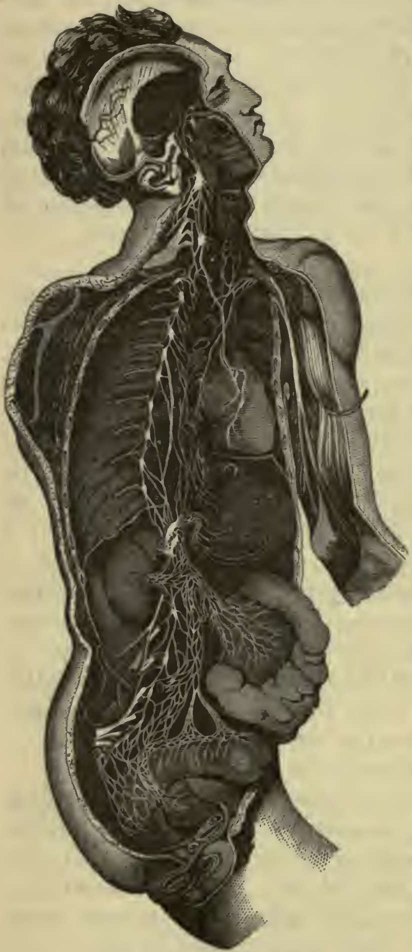
The first sympathetic ganglion in the head is the *ophthalmic ganglion*, in the orbit of the eye, on the outer aspect of the optic nerve. It communicates by slender filaments with the carotid plexus of sympathetic nerves, receives a motor root from the oculomotorius, and a sensitive root from the ophthalmic division of the fifth pair. Its filaments of distribution, known as the "ciliary nerves," pass forward upon the eyeball, pierce the sclerotic, and terminate in the iris.

The next is the *spheno-palatine ganglion*, in the spheno-maxillary fossa. It communicates, like the preceding, with the carotid plexus, receives a motor root from the facial nerve, and a sensitive root from the superior maxillary division of the fifth pair. Its filaments are distributed to the levator palati and uvular muscles, to the mucous membrane of the posterior part of the nasal passages, and to that of the hard and soft palate.

The third is the *submaxillary ganglion*, connected with the submaxillary gland. It communicates with the superior cervical ganglion of the sympathetic by filaments accompanying the external carotid and facial arteries. It derives its sensitive filaments from the lingual branch of the fifth pair, and its motor filaments from the facial nerve, by the chorda tympani. Its branches of distribution pass mainly to the submaxillary gland and duct.

The last sympathetic ganglion in the head is the *otic ganglion*, situated beneath the base of the skull, on the inner side of the inferior maxillary division of the fifth pair. It receives filaments of communication from the carotid plexus; a motor root from the facial by the small superficial petrosal nerve, as well as one or two short fibres from the inferior maxillary division of the fifth pair; and a sensitive root from the glossopharyngeal by the nerve of Jacobson. Its branches are sent to the internal muscle of the malleus in the middle ear (tensor tympani), to the circumflexus palati, and to the mucous membrane of the tympanum and Eustachian tube.

Fig. 128.



Ganglia and Nerves of the Sympathetic System.

The continuation of the sympathetic nerve in the neck consists of two and sometimes three ganglia, the superior, middle, and inferior, communicating with each other and the cervical spinal nerves. Its filaments follow the course of the carotid artery and its branches, forming by their inosculations the corresponding arterial plexuses, and supplying fibres of distribution to the thyroid gland, the larynx, trachea, pharynx, and œsophagus. By the superior, middle, and inferior cardiac nerves it also supplies fibres to the cardiac plexus, and through it to the heart.

In the chest, the communications of the sympathetic ganglia with the spinal nerves are double; each ganglion receiving two filaments from the intercostal nerve next above it. The nerves originating from the ganglia are distributed to the plexuses on the thoracic aorta, and to those of the lungs and œsophagus.

In the abdomen, the sympathetic system consists mainly of an aggregation of ganglionic enlargements situated on the cœliac artery, known as the *semilunar* or *cœliac ganglion.* From this centre a multitude of diverging and inosculating branches are sent out, which, from their common origin and radiating course, are termed the "solar plexus." Its secondary plexuses, accompanying the branches of the abdominal aorta, are distributed to the stomach, intestine, spleen, pancreas, liver, kidneys, supra-renal capsules, and internal organs of generation.

In the pelvis, there are four or five pairs of ganglia, situated on the anterior aspect of the sacrum, and, at its lower extremity, the "ganglion impar," which is regarded as a fusion of two symmetrical ganglia.

In all these parts a main characteristic of the sympathetic nerves is their arrangement in the form of plexuses, which surround the arterial branches, and follow their peripheral distribution in the vascular organs.

Sensibility and Motor Power in the Sympathetic System.

The sympathetic ganglia and nerves are endowed both with sensibility and the power of exciting motion; but these properties are less active than in the cerebro-spinal system, and are exercised in a different manner. If a motor or sensitive spinal nerve be irritated by the galvanic current, the evidences of pain or of muscular reaction are decisive and instantaneous. There is hardly an appreciable interval between the application of the stimulus and the sensation or motion which results. But in experiments on the sympathetic nerves, evidences of sensibility, when manifested, are much less acute, and show themselves only after prolonged application of the exciting cause.

The same character is exhibited in their motor action. If the semilunar ganglion or its nerves be galvanized, no immediate effect is visible; but after a few seconds a slow, progressive, vermicular contraction takes place in the intestine, and continues for some time after the galvanization has ceased.

Connection with the Special Senses.—In the head, the sympathetic has an important connection with the special senses. This is especially noticeable in the eye, from influences regulating the movements of the pupil. The reflex action, by which these movements take place, is transmitted by the oculomotorius nerve to the ophthalmic ganglion, and thence by the ciliary nerves to the muscular fibres of the iris.

The movements of the iris exhibit consequently a somewhat sluggish character, which indicates the intervention of the sympathetic system. They do not take place instantaneously with the variation of light, but require an appreciable interval of time If both eyes be closed and covered, long enough to allow complete dilatation of the pupils, and then suddenly opened, the pupils contract somewhat rapidly to a certain extent, and afterward continue to diminish for several seconds, until equilibrium is fairly established.

As the movements of the iris derive their stimulus, through the ophthalmic ganglion, from the oculomotorius nerve, if this nerve be divided between the brain and the eyeball, the pupil becomes sensibly dilated, and loses in great measure its power of contraction under the influence of light. There is a partial paralysis, in which the circular fibres of the iris are relaxed, while its radiating fibres continue to act, causing enlargement of the pupil.

On the other hand, if the sympathetic nerve be divided in the neck, or its superior cervical ganglion extirpated, the pupil on the corresponding side becomes contracted from paralysis of its radiating fibres. In quadrupeds, the eyeball is also drawn backward into the orbit, causing partial closure of the upper and lower eyelids, and advance of the third eyelid or "nictitating membrane" over the cornea. This recession of the eyeball is due to paralysis of a muscle composed of unstriped fibres, which exists in most quadrupeds under the name of the "orbital muscle," and which normally maintains the eyeball in a moderate state of protrusion. After its paralysis, the straight muscles of the orbit, being no longer antagonized, produce permanent retraction of the eyeball, and consequently partial closure of the lids. Both the closure of the lids and the narrowing of the pupil are therefore secondary effects of division of the sympathetic nerve.

But if, under these circumstances, the upper extremity of the divided nerve be stimulated by faradization, the conditions are reversed. The eyeball advances to its former place in the orbit, and the pupil contracts. Both these effects correspond in degree with the stimulation of the nerve. If the electric current be of moderate strength, the eye may be simply restored for the time to its normal condition. If of greater intensity, it may cause protrusion of the eyeball and reduction of the pupil to its minimum diameter. When faradization is suspended, the pupil again enlarges, and the eyeball returns to its retracted position.

It is evident, accordingly, that the muscular apparatus of the eye is under the control of two nervous influences, derived respectively from the cerebro-spinal and the sympathetic system. The iris receives all its motor fibres from the ophthalmic ganglion. But those causing contraction of the pupil come through this ganglion from the oculomotorius nerve: those causing dilatation are derived, through the same channel, from the central ganglia of the sympathetic system.

Vasomotor Nerves and Nerve Centres.

The most important general function of the sympathetic nerves and nerve centres is connected with the blood-vessels and the circulation in different regions of the body. Their filaments and plexuses are especially associated with the arterial branches, which they follow in their subsequent ramification; and their terminal fibres are largely distributed to the muscular coat of these vessels. Under their influence the muscular elements contract, thus approximating the walls of the artery, and diminishing its calibre. The nerves which excite in this way the contraction of the blood-vessels are called "Vasomotor nerves," and the nerve centres from which they emanate "vasomotor centres."

Muscularity and Contractility of the Blood-vessels.—So far as their structure is concerned, the arteries are, in great measure, muscular organs. Their middle coat, at least in those of medium and smaller size, contains unstriped muscular fibres mingled with elastic tissue; and the relative abundance of these fibres increases as the size of the artery diminishes, the middle coat of the smallest arterial branches being almost exclusively muscular. The fibres of this coat are wrapped round the artery in an annular direction; producing, when called into activity at any point, a local constriction of the arterial tube.

Furthermore, it is shown by observation that arteries, like other muscular organs, have the power of contractility. Their contraction in the living animal, under mechanical irritation or galvanic stimulus, has been demonstrated in various observations quoted by Milne Edwards,* and corroborated by Vulpian† in more extended experiments on the same subject. The carotid, femoral, hypogastric, interdigital, auricular, and mesenteric arteries, have all been seen to contract when touched with the point of a needle, rubbed with a smooth instrument, or subjected to the galvanic current. There are certain peculiarities in the phenomena thus produced, showing a physiological relationship between the arteries and other organs composed of unstriped muscular fibres. First, the contraction of the artery does not take place immediately on the application of the stimulus, but only after a perceptible interval. According to Vulpian, when the electrodes are placed for a few instants in contact with an artery, no effect may be visible on their withdrawal; but after a short time the vessel diminishes in size, becoming gradually smaller at the point of stimulation, until its calibre is nearly or quite obliterated. It remains in this condition for ten or fifteen seconds, after which it slowly enlarges to its previous size. Secondly, the contractility of the vascular walls under local stimulation is more distinct in the branches than in the trunks of the arteries, and is most pronounced in their smallest ramifications. This corresponds to the anatomical structure of these vessels, in which the muscularity of their middle coat increases with their diminution in size.

The contraction of an artery under these circumstances has an effect on the local circulation. The diminished calibre of the vessel allows a smaller quantity of blood to pass through it, and thus produces a partial anæmia of the region supplied by its branches. If this region be wanting in collateral inosculations, its change in vascularity may be very marked. All the vascular ramifications beyond the constricted portion of the artery become comparatively bloodless; and they continue in this condition until the artery relaxes, and again allows the free entrance of blood. While the entire system, therefore, depends on the heart as an organ of impulsion for the circulation in general, each artery controls, for its own special region, the quantity of blood admitted to the capillaries and veins.

Rhythmical Contraction of Arteries in Particular Parts.—If the ear of a white rabbit be held for a few moments against the light it will be seen that its blood-vessels change their appearance from time to time, and that this change occurs with a certain regularity. The cen-

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* Leçons sur la Physiologie et l'Anatomie Comparée. Paris, 1859, tome iv., p. 207.

† Leçons sur l'Appareil Vasomoteur. Paris, 1875, tome i., p. 43.

tral artery, as it passes from the base of the ear toward its apex, divides into branches supplying the capillary plexus; and the vessels emerging from this plexus unite in two principal veins, which return along the edges of the organ toward its base. Both the central artery with its branches, and the principal veins, are readily visible by transparency, while the intervening tissue has a light rosy hue, from the blood in the capillary circulation. The change in vascularity, first observed by Schiff,* takes place in the following manner: The central artery diminishes in size, becoming narrower and fainter, until nearly invisible Its branches disappear, the ear generally becomes more pallid, and the veins, receiving from the capillaries a smaller quantity of blood, appear less numerous and less distinct. The circulation in the organ is thus reduced in quantity at least one-half. This condition lasts for eight or nine seconds, after which the artery begins to enlarge. A thread-like stream of blood enters it from below, increasing in thickness and capacity, and extending rapidly upward into the arterial ramifications. The tissues regain their rosy color, and the veins become prominent along the edges of the organ. The artery is then in a state of diastole, supplying the ear with a full quantity of blood. It remains in this condition for two or three seconds, when another contraction takes place, and the circulation is again reduced. These alternations of constriction and expansion recur usually about ten or twelve times per minute. They are not strictly uniform either in extent or frequency, but they take place with sufficient regularity to show that they are not accidental, but depend on causes of internal origin.

It is probable that other organs, if they could be examined by transparency, would show a similar variation in vascularity. The small saphenous artery in the rabbit has been seen by Loven, Riegel, and Vulpian to exhibit alternate movements of constriction and dilatation once or twice per minute. In examining the circulation in the frog's foot under the microscope, the small arteries sometimes show a local constriction by which they are reduced in diameter for a certain time, afterward enlarging to their former size; and temporary changes of vascularity in the glandular organs or the mucous membranes have long been known to take place in connection with secretion or digestion.

Contraction and Dilatation of Arteries under Nervous Influence.—When the sympathetic nerve is divided in the neck, one of the most immediate and striking effects is a vascular congestion in the parts above, on the corresponding side. This effect may be produced in any warm-blooded animal, but is especially manifest in the ear of the white rabbit, where the vascularity is easily examined by transparency, and where the corresponding parts on the two sides can be directly compared with each other. A few minutes after section of the nerve all the vessels of the ear on the affected side become turgid with blood. The artery enlarges, its branches become more visible, the tissues gen-

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* Comptes Rendus de l'Académie des Sciences. Paris, 1854, tome xxxix, p. 508.

erally are ruddy in color, and the marginal veins are increased in size; while many venous branches, which were before imperceptible, become distinctly apparent. The artery no longer exhibits its periodical constrictions, but remains in a state of permanent diastole, and the quantity of blood circulating in the ear is consequently increased.

A variety of secondary consequences follow from this condition. First, the temperature of the ear is increased. A larger quantity of blood from the interior of the body, passing through the vessels, communicates its warmth to the tissues of the part, and the elevation of temperature is perceptible both by the touch and the thermometer. Secondly, the blood in the veins becomes brighter, since in its more rapid passage through the capillaries it loses less oxygen, and consequently retains more nearly the hue of arterial blood. Thirdly, the sensibility of the parts is increased and reflex actions from irritation of the integument are more strongly pronounced.

These results are not confined to the ear, but extend to all parts of the head and face on the side of the section. The skin, the conjunctiva, the mucous membranes of the mouth and nasal passages, even the meninges of the brain, and, according to Vulpian, the fundus of the eye when examined by the ophthalmoscope, all show an increased vascularity and more abundant circulation.

The phenomena above described are increased in intensity by extirpation of the superior cervical ganglion of the sympathetic. They are due to paralysis of the muscular coat of the arteries in the regions supplied by sympathetic filaments from this source. Owing to this paralysis, the arteries no longer offer their usual resistance to the pressure of blood from the heart. Their relaxation admits a larger quantity to the capillaries of the corresponding regions, and thus causes an increased local circulation.

These effects of division of the sympathetic are all reversed by its stimulation. If the upper extremity of the divided nerve be subjected to faradization, the arteries of the affected ear diminish in size, the vascular congestion disappears, and the local temperature becomes reduced to its normal standard, or even lower. The varying condition of the blood-vessels under nervous influence is shown by an experiment of Bernard,* in which the upper part of a rabbit's ear is cut off by a clean incision, allowing the blood to escape in jets from the divided arteries. The force and height of the jets having been observed, the sympathetic nerve is divided in the neck on the corresponding side. The blood at once escapes from the wounded ear in greater abundance, and the arterial jets rise to double or triple their former height. The galvanic current is then applied to the nerve, above the point of section, when the streams of blood escaping from the wound diminish or disappear; but they recommence when the galvanization of the nerve is suspended.

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*Journal de la Physiologie. Paris, 1862, p. 397.

The sympathetic nerves accordingly exert an influence on the muscular coat of the arteries similar to that of the cerebro-spinal nerves on the voluntary muscles. They cause contraction of these vessels, a diminished flow of blood through them, and consequently pallor and coolness in the corresponding parts. On the other hand, division of these nerves causes relaxation of the arteries and all the secondary results of an increased supply of blood.

Centres of Origin of the Vasomotor Nerves.—From facts above detailed it is evident that the vasomotor nerves of the head and face come from below. They ascend in the cervical portion of the sympathetic nerve, and pass, through the superior cervical ganglion, to their distribution in the blood-vessels. The superior cervical ganglion is itself, in some degree, a source of power for these nerves; and its extirpation produces complete and durable vascular relaxation in the parts above. But it receives at least a portion of this power from the sympathetic nerve in the neck; since division of the nerve below the ganglion is sufficient to cause a distinct congestion in the corresponding parts.

The real origin of the vasomotor fibres of the sympathetic is in the spinal cord. All the sympathetic ganglia, beside their connection with each other by the longitudinal filament of the sympathetic nerve, are connected with the adjacent spinal nerves by communicating branches; and many of the fibres composing these branches may be traced, through the spinal nerve roots, to the spinal cord. Furthermore, experiment also shows that the spinal cord is the source of nervous action for the sympathetic system.

This was first proved by Budge and Waller * in regard to the action of the sympathetic on the radiating fibres of the iris. They found in the rabbit a region in the spinal cord, extending from the first cervical to the sixth dorsal vertebra, within which galvanization produces dilatation of the pupil, as if the sympathetic itself had been galvanized; but if the sympathetic be previously divided in the neck on one side, galvanization of the cord is without effect on the pupil of the corresponding eye, while it still causes dilatation on the side where the sympathetic is entire. The stimulus therefore passes, in this instance, through the spinal nerve roots and their branches to the ganglia at the root of the neck, and thence upward, through the cervical portion of the sympathetic to the head. The part of the spinal cord where galvanization produces its maximum effect on the pupil is that included between the second and third dorsal vertebræ.

It was subsequently shown by Bernard † that the vasomotor fibres for the head emanate from the spinal cord in the same region, but at a slightly different level; so that the fibres going to the iris and those influencing the blood-vessels are distinct though adjacent in their origin from the cord. If, in the dog, the roots of the first two dorsal nerves be divided within the spinal canal, all the phenomena connected

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* Comptes Rendus de l'Académie des Sciences. Paris, 1851, tome xxxiii., p. 372.

† Ibid., 1862, tome lv., p. 383.

with the pupil and eyeball follow in the same way as if the sympathetic had been cut in the neck, but there is no vascular congestion or increased temperature of the parts; and galvanization of the peripheral extremities of the divided nerve roots, causes dilatation of the pupil, like galvanization of the sympathetic in the neck. On the other hand, if the trunk of the sympathetic be divided in the upper part of the chest, between the heads of the second and third ribs, there is no contraction of the pupil, but the temperature of the ear is increased from 4° to 6° C. above that of the opposite side.

There is accordingly a remarkable difference between the nerve fibres for sensation and voluntary motion and those for the blood-vessels in the route which they follow to their distribution in the head. The sensitive and motor nerves of the head and face emerge from the base of the brain and pass, through the cranial foramina, to the integument and muscles. Those destined for the blood-vessels are given off from the spinal cord, mainly with the roots of the third pair of dorsal nerves, whence they join the sympathetic, passing upward through its cervical portion to the head and face.

There is also a difference of origin, though less marked, between the fibres for sensation and volition and those for vasomotor action in the limbs. The vasomotor fibres for the upper limb do not originate with the nerve roots going to form the brachial plexus, but farther down, in the dorsal portion of the cord. Bernard found that, in the dog, division of the last three cervical and first two dorsal nerves within the spinal canal causes paralysis of motion, and sensation in the corresponding foreleg, but no vascular congestion or calorification. On the other hand, extirpation of the first thoracic ganglion of the sympathetic, or section of the nerves of the brachial plexus after they have been joined by filaments from this ganglion, causes an elevation of temperature in the corresponding limb; and the same result follows division of the thoracic portion of the sympathetic between the third and fourth dorsal vertebræ. The vasomotor fibres paralyzed by this section come therefore from below the first thoracic ganglion; and, according to Cyon, they emanate from the spinal cord with the roots of the dorsal nerves, from the third to the seventh pairs inclusive.

The vasomotor fibres for the lower limb have a similar origin. According to Bernard, section of the spinal nerve roots destined for the lumbo-sacral plexus, in the dog, paralyze the corresponding hind leg without causing increase of temperature; but the latter effect is produced in addition by dividing the sympathetic at the level of the fifth and sixth lumbar vertebræ, or by section of the sciatic nerve. The vasomotor fibres of the limbs are therefore distinct from those which supply them with ordinary motion and sensibility.

Tonic Contraction of Blood-vessels and its Influence on the Circulation.—Under the stimulus of the sympathetic fibres distributed to the arterial walls, the vessels are normally maintained in a moderate state of contraction. This continuous muscular activity is the "tone" or tonic contraction of the arteries, by which they offer a certain resistance to the pressure of the blood. The blood moves accordingly under the influence of two opposite forces, namely: First, the cardiac impulse, which tends to urge it rapidly through the circulation; and secondly, the tonic arterial resistance, which tends to delay its passage into the capillary vessels. The tonic arterial contraction varies with the nervous influences which control it; and in this way the local activity of the circulation is increased or diminished. There appears to be furthermore a compensating action in this respect, between the blood-vessels of different parts. When the arteries of one organ are contracted, diminishing the quantity of blood which it contains, vascular pressure must be increased in the neighboring parts, unless a proportionate enlargement of their blood-vessels restores the normal relation between them. But when the vascular tone is abolished in any region by division of its sympathetic nerves, its blood-vessels yield to the pressure of the rest of the arterial system, and remain in a state of turgescence and relaxation.

Dilator Nerves.—Beside the nerve fibres which cause contraction of the blood-vessels, there are others which cause their dilatation. The latter class, which, from their mode of action, are called "dilator nerves," do not all pass through the sympathetic system, but are distributed from the cerebro-spinal nerves to the vascular organs.

The most striking and earliest known instance of the action of a dilator nerve is that of the pneumogastric in connection with the heart (page 489). This action is characterized essentially as follows: 1st. Galvanization of the nerve causes relaxation of the heart, and consequently its dilatation by blood flowing in from the large veins; 2d. If the nerve be divided and galvanization applied to its peripheral extremity, the same effect is produced, showing that the influence is direct in its operation, following a centrifugal course through the nerve to the heart.

A similar action is exerted on the circulation in the tongue and submaxillary gland. These observations, first made by Bernard,* have been corroborated and extended by subsequent experimenters, and especially by Vulpian.†

The vascular supply of the tongue and submaxillary gland receives nerve fibres from two sources, namely: 1st, sympathetic fibres coming from the carotid plexus and passing with the arterial branches to their distribution; and 2d, fibres coming from the facial nerve through the chorda tympani, which join the lingual branch of the fifth pair, and are thence distributed to the tongue and submaxillary gland. The influences exerted by these two sets of fibres on the vascularity of the parts are the opposite of each other. Section of the sympathetic filaments causes relaxation of the blood-vessels, increased circulation, ruddy color of the venous blood, and abundant salivary secretion; while galvanization of their peripheral extremity produces contraction

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* Leçons sur les Liquides de l'Organisme. Paris, 1859, tome i., p. 312.

† Leçons sur l'Appareil Vasomoteur. Paris, 1875, tome i., p. 153.

of the blood-vessels and general reversal of the foregoing results. But if either the lingual nerve, or the chorda tympani above its junction, be divided, the effect is a diminution of the circulatory current both in the tongue and submaxillary gland. On the other hand, galvanization of the peripheral extremities of these nerves causes dilatation of the blood-vessels, and all the phenomena of increased circulation.

It must be admitted, accordingly, that the dilator nerves exert a direct local influence which causes relaxation of the blood-vessels. The mechanism of this influence is not easily understood; since the only muscular fibres connected with the arteries surround them in a circular direction, and could produce by their contraction no other effect than a narrowing of the arterial tube. The action of the dilator nerves can only be explained as an "action of arrest." They convey from the nervous centres outward an influence which for the moment interrupts the tonic contraction of the blood-vessels. Owing to this suspension of tonicity, the vessels dilate under the pressure of the blood, and allow it to circulate in larger quantity. When the suspensive action is terminated, the normal stimulus of the sympathetic fibres restores the tonicity of the blood-vessels, and the circulation returns to its ordinary condition.

The action of arrest, as a nervous phenomenon, is not confined to the vascular system. All the sphincters exhibit it in a marked degree. These muscles are habitually in a state of tonic contraction, by which they keep the outlets of the body closed without voluntary effort. But when evacuation of the rectum or bladder is to take place, the first step in the process is an influence proceeding from the spinal cord, which suspends the contraction of the sphincters; and after their relaxation, the expulsion of the urine or feces is effected by other muscles. Wherever antagonistic muscles exist, it is evident that the contraction of one, to be effective, must be accompanied by the relaxation of its opposite; and in all voluntary movements, the relaxation of one set of muscles is as prompt and as accurately adjusted as the contraction of the other. It is probable that the action of arrest plays an important part in the nervous operations generally; but it is most distinctly manifest in the dilator nerves of the vascular system.

Reflex Contraction and Dilatation of the Blood-vessels.—Thus far the variations in calibre of the blood-vessels have been shown, in experimental observations, to depend on the immediate action of the vasomotor and dilator nerves. But in the living body these variations are habitually reflex in their mode of production. The vascular contraction or dilatation which shows itself in a particular area, is due to the impression received by a sensitive surface, conveyed inward to some nervous centre of the vasomotor system, and thence reflected in a centrifugal direction to the blood-vessels. The most frequent instance of reflex vascular constriction is that which follows irritation of the central extremity of a sensitive nerve. This effect has been observed by many experimenters, and is regarded as nearly invariable. Galvanization of the central extremity of the sciatic nerve causes general constriction of the blood-vessels throughout other parts of the body, indicated by increased arterial pressure. A similar result is produced by irritation of the trigeminus or other sensitive nerves or nerve roots, or by that of extended regions of the integument. According to Vulpian,* this effect is very observable, in dogs, on the under surface of the tongue after division of one sciatic nerve. On galvanizing the upper extremity of the nerve, the under surface of the tongue grows paler, and its superficial veins diminish visibly in size, or even become imperceptible. This action, which is first conveyed by the sciatic nerve to the spinal cord, is finally transmitted to the tongue through the fibres of the sympathetic; since if the sympathetic be divided in the cervical region, the above results are no longer produced on that side from irritation of the sciatic nerve.

Reflex dilatation of the blood-vessels is also of frequent occurrence. It is distinctly manifested in the rabbit's ear on galvanizing the central extremity of the anterior cervico-auricular nerve after its division. This effect, formerly observed by Schiff and Rouget, is, according to Vulpian, one of the easiest to reproduce; especially if the animal be first poisoned by woorara, which suspends the action of the voluntary muscles, and prevents their interfering with the blood-vessels by local contraction. Reflex vascular dilatation is also the usual accompaniment of local injuries or irritations. Congestion soon shows itself in the neighborhood of any wound in the integument or subcutaneous tissues; and the intestines, when exposed by opening the abdominal cavity, become rapidly covered with an increased vascularity.

The most familiar examples of reflex dilatation are those occurring in the glands and mucous membranes at the time of their functional excitement. These organs present alternate conditions of repose and activity. In the former condition their blood-vessels are moderately contracted, supplying blood in small quantity for the nutrition of the glandular tissues, or for the preparation of their special organic ingredients. But when the period arrives for active secretion, there is a dilatation of the blood-vessels, with increased local circulation and free exudation of the secreted fluids. This phenomenon was witnessed in the mucous membrane of the stomach, so long ago as in the observations of Beaumont* on the gastric fistula of Alexis St. Martin; and it has subsequently been observed in many similar cases. In the submaxillary gland of the dog, reflex vascular congestion is at once produced by introducing vinegar into the mouth, or by any stimulus which excites the salivary secretion. A similar variation was found by Bernard in the vascularity of the pancreas and duodenum, in the dog, under the conditions of fasting and digestion. In the intervals of digestion these organs are pallid, with but few blood-vessels visible upon their surface. But after the introduction of food, and while digestion is going on, their appearance is greatly changed. The

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* Leçons sur l'Appareil Vasomoteur. Paris, 1875, tome i., p. 238.

† Experiments and Observations upon the Gastric Juice. Boston, 1834.

smaller arteries are more abundantly visible, their curvatures more pronounced, and their pulsations more strongly marked. The superficial veins are also increased in size and apparent numbers, and the intervening tissues have a ruddy color, due to the abundant circulation in their capillary vessels. This condition lasts for a certain time, while secretion and digestion are in progress; after which it gradually subsides, and the circulation returns to its former state of comparative inactivity.

It is evident that these reflex actions take place in some nervous centre, in which the centripetal impression is converted into a centrifugal impulse. It appears that the ganglia of the sympathetic system act in some measure as nervous centres for this purpose. This is indicated by the fact that the vascular paralysis of the head and face, following division of the sympathetic nerve in the neck, is more pronounced if the superior cervical ganglion be extirpated; and, as a general rule, removal or destruction of the sympathetic ganglia produces more effect than simple section of the nerve trunk. According to Vulpian, after removal of the entire brain and the upper half of the spinal cord, including the origin of the brachial nerves, in the frog, extirpation of the cervical ganglion of the sympathetic is followed by vascular congestion of the corresponding half of the tongue and buccal cavity. The sympathetic ganglia have therefore a certain influence as the sources of nervous power for vascular parts.

But the action of these ganglia is limited in importance, and affects only the parts to which their fibres are directly distributed. It has already been shown that the roots of the sympathetic system emanate from the spinal cord, and that they emerge from it at special points for the head and limbs respectively. There is reason to believe that they traverse the cord for some distance before detaching themselves from its surface, and that their source in the gray substance is at a higher level. According to numerous observers, a transverse section of the cord in the cervical region causes marked vascular relaxation throughout the body, as if all the vasomotor fibres had been divided in descending from above. This effect is produced by transverse sections of the cerebro-spinal axis at any level in the cervical portion of the cord or in the medulla oblongata, nearly to the posterior edge of the tubercula quadrigemina; but not by sections above that point. It is accordingly maintained by some physiologists (Schiff, Owsjannikow, Liégeois) that there is a common centre for all the vasomotor fibres of the body, situated in the medulla oblongata or immediately above. In the opinion of others (Brown-Séquard, Vulpian) the vasomotor centres are more widely scattered in the cerebro-spinal axis; since reflex modifications of vascularity may still be produced to some extent after division of the spinal cord in the cervical region, and even certain lesions in the cerebral hemispheres seem to produce vascular congestion in the limbs or internal organs. This question is not positively determined; but it appears certain that the main centres of reflex action for the vascular system are in the cerebro-spinal axis, whence their nerve fibres are distributed, by various routes, to all parts of the body.

CHAPTER VIII.

THE SENSES.

THE senses are the endowments by which we gain perception of external objects and phenomena. They are consequently the primitive source of all information, and the channels of all conscious relation with the external world. The term *sensation* indicates the perception of any impression from without, of whatever nature. The *senses*, on the other hand, are subdivisions of the main function, each devoted to a particular class of phenomena. They are five in number, namely: 1. General sensibility. 2. The sense of taste. 3. The sense of smell. 4. The sense of sight. 5. The sense of hearing.

General Sensibility.

General sensibility is the faculty by which we appreciate the simpler physical properties of external objects, such as their consistency, surface, temperature, and mass. It exists throughout the general integument, and in the mucous membranes near the exterior. Notwithstanding that it includes several different impressions, they are all, so far as we know, communicated by the same nerves; and the grade of sensibility for all varies in the same direction and to the same degree in different parts of the body. The sensations thus produced, though presenting certain differences from each other, are therefore associated under the head of general sensibility.

Sense of Touch.—This is, perhaps, the simplest form of sensory impression, and is known as "tactile sensibility." It is produced by the contact of foreign bodies with the sensitive surface, and gives information as to their solidity, configuration, and indifferent or irritating qualities. There is a certain variety in these impressions, but they evidently belong to the same group. There is no essential difference in the effect of sharp-pointed instruments or irritating substances applied to the skin, the passage of the galvanic current, pungent liquids in contact with the tongue, or pungent vapors in the nasal passages. They are all impressions of tactile sensibility, and depend on a similar irritation of the nervous extremities.

The grade of tactile sensibility varies in different regions. The method adopted for appreciating this variation consists in applying to the skin or mucous membrane the points of a pair of compasses, tipped with small pieces of cork. If the two points be a very short distance apart, they cannot be accurately distinguished from each other, and the two sensations are blended into one. The minimum distance at which the points can be distinguished thus indicates the grade of sensibility at that spot. The observations of Valentin* give the following as the limits of distinct perception in different regions:

DISTANCE AT WHICH TWO POINTS MAY BE SEPARATELY DISTINGUISHED.

At the tip of tongue	1.00	millimetre.
" palmar surface of tips of fingers	1.50	"
" " " of second phalanges	3.24	"
" " " of first phalanges	3.44	"
" dorsum of tongue	5.22	"
" dorsal surface of fingers	8.12	"
" cheek	9.46	"
" back of hand	14.50	"
" skin of throat	17.27	"
" dorsum of foot	26.10	"
" front of sternum	33.07	"
" middle of back	50.43	"

This method does not necessarily measure the *acuteness* of sensibility, since the two points might be less easily distinguished from each other in any one region, and yet the intensity of the sensation produced might be as great as in the surrounding parts; but it affords an estimate of the *delicacy* of tactile sensation, by which we distinguish slight inequalities of surface in foreign bodies. There is reason, however, to believe that the two qualities correspond with each other in development in various localities; and tactile sensibility is frequently found to be most delicate where the amount of sensation is also greatest. A feeble galvanic current may be perceived at the tips of the fingers, though it may produce no impression on the limbs or trunk; and one too faint to be distinguished by the fingers may be perceptible at the tip of the tongue.

Certain parts of the body, furthermore, are especially suitable for organs of touch, not only from their acute sensibility, but also on account of their conformation and mobility. In man, the hands are the most favorably constructed for this purpose, owing to the varied movement of the fingers, by which they may be applied to surfaces of any form, and brought successively in contact with all their parts.

In some animals, the long bristles on the lips are used for this purpose, each bristle being connected at its base with a nervous papilla; and in the elephant the end of the nose, developed into a flexible and sensitive proboscis, is the principal organ of touch. This function, therefore, may be performed by any part of the body where the accessory organs are sufficiently developed.

In the head and face, the sensibility of the skin is dependent on the branches of the fifth pair. In the body and limbs it is due to the sensitive fibres of the spinal nerves. It exists, to a considerable extent, in the mucous membranes of the mouth and nose, and other passages

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* Todd's Cyclopædia of Anatomy and Physiology, vol. iv., article Touch.

leading to the interior. Sensibility is most acute in mucous membranes supplied by the fifth pair, namely, in the conjunctiva, anterior part of the nares, inside of the lips and cheeks, and the anterior two-thirds of the tongue. It diminishes from without inward, and disappears altogether in the internal organs not abundantly supplied with cerebro-spinal nerves.

Sensations of Temperature.—The appreciation of temperature is, in general, most highly developed in parts which have the greatest tactile sensibility. The difference in this respect between the sensitive integument of the face and the comparatively insensible scalp is very marked; and hot applications may be readily borne by the scalp which would be intolerable upon the face. The extent of surface exposed has also an influence on the effect produced by temperature; and a moderate degree of warmth or cold applied over a large area is more readily perceived than if confined to a limited region. There is evidence that the impressions of temperature and those of touch are either transmitted by different nerve fibres, or depend on different forms of nervous excitement; since, according to Brown-Séquard,* there are instances in which the two kinds of sensibility are impaired independently of each other. In some forms of paralysis, tactile sensibility may be lost while that of temperature remains; or, on the other hand, the power of appreciating temperature may disappear while impressions of contact are still perceived.

Sensations of Pain.—The sense of pain is different in character from that caused by tactile impressions or variations in temperature. It is produced by exaggerated mechanical irritation or by excessive heat or cold; and in most instances, when the intensity of an impression rises above a certain point, the ordinary perceptions disappear, and that of pain takes their place. Thus if the blade of a knife or the point of a needle be placed gently in contact with the skin, we perceive, by tactile sensibility, its qualities of form and surface. But if the pressure be increased beyond a certain degree, or if the integument be wounded, we have no further perception of the physical properties of the foreign body, and are only conscious of the pain which it inflicts. The appreciation of cold or warmth, in like manner, is only possible within moderate limits; and when either is so excessive as to produce pain, all accurate notion of the degree of temperature is lost. The contact of a red-hot iron and that of one much below the freezing-point of water produce sensations not essentially different from each other, and marked only by their painful character.

The sense of pain may be preserved or lost independently of other kinds of sensibility. The anæsthesia produced by ether or chloroform may be carried to such a point that the capacity for feeling pain is abolished, while tactile sensibility remains; and in this condition the

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* Physiology and Pathology of the Central Nervous System. Philadelphia, 1860, pp. 84, 98, 125.

wounds caused by puncturing or cutting instruments may be felt, unaccompanied by any sense of suffering. Similar observations have been made in cases of paralysis, where the patient can sometimes perceive the contact of foreign bodies without experiencing any painful sensation; or, on the other hand, the sense of pain may persist, while that of touch is diminished or lost. Notwithstanding this apparent independence of the necessary conditions for the sensation of pain, it is transmitted by the same nerves which convey ordinary impressions; and those which, like the branches of the fifth pair, are endowed with the most acute tactile sensibility, are also capable, in injury or disease, of giving rise to the severest painful impressions.

Mode of Action of the Senses in general.—There are certain facts connected with general sensibility, and common to the operation of all the senses, which are of sufficient importance to be considered by themselves.

In the first place, an impression of any kind, made upon a sensitive organ, *remains for a time after the removal of its exciting cause.* The excitement produced in the nerve fibres has a certain persistence, which is longer in some cases than in others, but which exists to some extent in all. The pressure of a foreign body upon the skin, especially if somewhat forcible and continued, is felt for a perceptible interval after the foreign body is removed. The sense of cold or warmth, from the contact of ice or heated liquids, lasts more or less after their application is discontinued. Even for the senses of sight and hearing, the same fact may be verified; and the duration of the nervous impression, though very short, has been found susceptible of measurement.

Secondly, the organs of sense after a time *become accustomed to a continued impression,* so that it is no longer perceived. If a uniform pressure be exerted on any part of the body, it at last fails to attract notice, and we become unconscious of its existence. In order to again excite a sensation, the pressure must be increased or diminished, or changed in locality or direction.

The olfactory apparatus also becomes habituated to odors, whether agreeable or disagreeable. A continuous and uniform sound, like the rumbling of carriages, or the hissing of boiling water, becomes after a time inaudible; but when the sound ceases our attention is excited by the change. The senses, accordingly, receive their stimulus as much from the variation and contrast of external impressions as from the impressions themselves.

Sense of Taste.

The sense of taste is, in some measure, intermediate in character between general and special sensibility. The organ by which it is exercised is furnished with vascular and nervous papillæ analogous to those of the general integument. Its mucous membrane is also endowed with general sensibility. Although it is highly probable that certain minute formations in its epithelial layer, known as "taste buds," may be especially connected with the perception of savors, there is thus far no certainty in this respect; and in any case the tactile and gustatory sensibilities are closely intermingled in the mucous membrane. The sensibility of taste, furthermore, is not confined to the fibres of a single nerve, but resides in portions of two, which also supply general sensibility to the corresponding parts; and lastly, though some gustatory impressions are of a distinctly special character, others, like the taste of oily or mucilaginous substances, differ but little from those of tactile sensibility.

The sense of taste is localized in the mucous membrane of the tongue, the soft palate, and the pillars of the fauces. The tongue is a flattened, leaf-like muscular organ, attached to the symphysis of the lower jaw in front, and to the os hyoides behind. It has a vertical sheet of fibrous tissue in the median line serving as its framework, and is provided with longitudinal, transverse, and radiating muscular fibres, by which it can be protruded or retracted, or moved in a lateral direction.

The lingual papillæ are of three kinds. First the *filiform papillæ*, which are the most numerous, and which cover most uniformly the upper surface of the tongue. They are long and slender, covered with horny epithelium, and usually prolonged into filamentous tufts. Secondly, the *fungiform papillæ*. These are thicker and larger than the foregoing, of a club-shaped figure, and covered with soft epithelium. They are most abundant at the tip of the tongue, but may be seen elsewhere on the surface of the organ, scattered among the filiform papillæ. Thirdly, the *circumvallate papillæ*. These are the rounded eminences, eight or ten in number, which form the V-shaped figure near the foramen cæcum. Each consists of a central eminence, surrounded by a wall or circumvallation, from which they derive their name. The circumvallation, as well as the central eminence, has a structure similar to that of the fungiform papillæ.

The sensitive nerves of the tongue are two in number, namely, the lingual branch of the fifth pair, and the lingual portion of the glossopharyngeal. The lingual branch of the fifth pair enters the tongue at the anterior border of the hyoglossal muscle. Its branches pass from below upward and from behind forward, between the muscular bundles of the organ, until they reach its mucous membrane, where their fibres penetrate the lingual papillæ.

The lingual portion of the glossopharyngeal nerve passes into the tongue below the posterior border of the hyoglossus muscle. It then divides into branches, which pass through the muscular tissue, and are distributed to the mucous membrane of the base and sides of the organ.

The mucous membrane of the base of the tongue, of its edges, and of its under surface near the tip, as well as that of the mouth and fauces generally, is also supplied with mucous follicles furnishing a viscid secretion by which its surface is lubricated. The muscles of the tongue are animated exclusively by filaments of the hypoglossal nerve.

The *exact seat* of the sense of taste has been determined by placing in contact with different parts of the mucous membrane a small sponge, moistened with a sweet or bitter solution. The experiments of Dugès, Vernière, and Longet, have shown that taste resides in the whole upper surface, the point and edges of the tongue, the soft palate, fauces, and part of the pharynx. The base, tip, and edges of the tongue possess the greatest amount of sensibility to savors, the middle portion of its dorsum less, and its under surface little or none. As the whole anterior part of the organ is supplied by the lingual branch of the fifth pair, and the whole of its posterior portion by the glossopharyngeal, it follows that the sense of taste is derived from both these nerves.

A distinction is to be made, in the action of foreign substances taken into the mouth, between the *special impressions derived from their sapid qualities*, and the *general sensations produced by their ordinary physical properties*. As the same substance is often capable of exciting both tactile and gustatory impressions, they are sometimes liable to be confounded with each other. The qualities which we perceive by the special sense of taste are savors, designated by the terms *sweet*, *bitter*, *salt*, *sour*, *alkaline*, and the like. Beside these, however, there are other qualities, which partake largely of the nature of ordinary physical properties, appreciable by means of general sensibility. A *starchy*, *oily*, or *mucilaginous* taste, when uncomplicated with additional savors, is but little different in kind from tactile impressions. The quality of *pungency*, communicated to the food by certain condiments, as pepper or mustard, is appreciated altogether by the general sensibility. The *styptic* taste seems to be an ordinary astringent effect combined with a peculiar excitement of the gustatory nerves, analogous to that caused by the galvanic stimulus.

Furthermore, the taste or *savor* of a substance is to be distinguished from its odoriferous properties or *flavor*. In most aromatic liquids, such as tea, coffee, and wine, a great part of the effect produced is due to the aroma or smell which reaches the posterior nares in the act of swallowing. Even in many kinds of solid food, such as freshly cooked meats, odor has an important share in the impression on the senses. If, during the deglutition of such substances, the nares be closed, so as to suspend in great measure the sense of smell, their flavor becomes nearly imperceptible; and a similar effect is produced by catarrhal inflammation of the nasal passages, which impairs for the time the sensibility of the olfactory membrane.

Necessary Conditions of the Sense of Taste.—There are certain conditions requisite for gustatory impressions, beside the integrity of the organ by which they are received.

First, the sapid substance, in order that its taste may be perceived, must be *in solution*. So long as it remains solid, however marked a savor it may possess, it gives no other impression than that of a foreign body in contact with the tongue. But if applied in a liquid form, it spreads over the mucous membrane, and its taste is perceived. Thus it is only the liquid and soluble portions of the food which are tasted, such as the animal and vegetable juices and the soluble salts. Saline substances which are insoluble, such as calomel or lead carbonate, produce no gustatory impression.

The mechanism of taste is, in all probability, direct and simple. The sapid substances in solution are absorbed by the lingual papillæ, and, coming in contact with the terminal nervous filaments, excite sensibility by uniting with their substance. The rapidity with which endosmosis will take place under certain conditions is sufficient to account for the quick perception of sapid substances introduced into the mouth.

It is on this account that *free secretion of saliva* is favorable to the gustatory function. If the mouth be dry, food has but little taste. But when the saliva is freely secreted, it is mixed with the food in mastication, assisting the solution of its sapid ingredients; and the fluids of the mouth, impregnated with the savory substances, are absorbed by the mucous membrane and excite the gustatory nerves.

An important part is taken in this process by the *movements of the tongue.* By these movements the food is carried from one part of the mouth to another, compressed against the mucous membrane, its solution assisted, and the penetration of fluids into the papillæ more rapidly accomplished. If powdered sugar, or a semi-solid bitter extract, be simply placed upon the dorsum of the tongue, little or no effect is produced; but when pressed by the tongue against the roof of the mouth, in the movements of eating or drinking, its taste is immediately perceived. This is explained by the well-known fact that movement and friction facilitate the liquefaction and imbibition of soluble substances. The nervous papillæ of the tongue may therefore be regarded as the essential instruments of taste, and the lingual muscles as its accessory organs.

Impressions of taste made upon the tongue *remain for a certain time afterward.* When a very sweet or a very bitter substance is taken into the mouth, its taste is retained for several seconds after it has been ejected or swallowed. Consequently, if different savors be presented to the tongue in rapid succession, they become undistinguishable, and produce only a confused combination of several impressions.

If the substance first tasted have a particularly marked savor, its impression will preponderate over that of the others. A similar effect is produced by substances which excite the general sensibility of the tongue, such as acrid or stimulating powders; and it belongs, in the greatest degree, to substances which are at the same time sapid, pungent, and aromatic, like sweetmeats flavored with the volatile oils. Advantage is sometimes taken of this in the administration of disagreeable medicines. By first taking into the mouth some highly flavored and pungent substance, nauseous drugs may be immediately swallowed with but little perception of their qualities.

Sense of Smell.

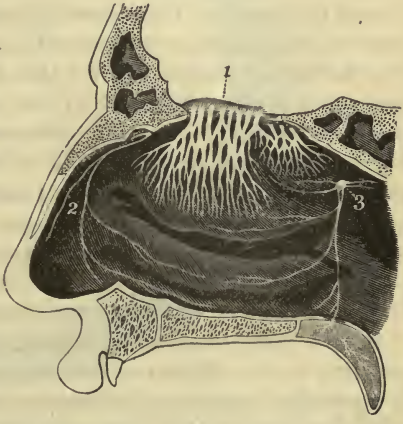
The distinguishing character of this sense is that it appreciates the quality of *gaseous or vaporous* substances. It can therefore detect odoriferous matters at a distance, and when concealed from sight. It differs, furthermore, from the sense of taste in being more distinctly localized; since it is confined to the upper portion of the nasal passages and depends on the filaments of a single pair of nerves.

The mucous membrane covering the superior and middle turbinated bones and the upper part of the septum nasi, which is alone capable of receiving odorous impressions, is known as the *olfactory membrane.* It is distinguishable from that lining the rest of the nasal passages: 1st, by its color, which in man, the sheep, and the calf is yellow, but in most other mammalia has a brownish tinge; 2dly, by its softer consistency; 3dly, in the greater thickness of the whole membrane, and especially of its epithelial layer. According to Kölliker, the epithelium of the olfactory membrane, in the sheep and rabbit, is about sixty per cent. thicker than that of the remaining nasal membrane. In most quadrupeds the epithelium of the nasal mucous membrane generally is covered with vibrating cilia, which are absent in the olfactory portion; but in man cilia are also found in the olfactory portion. This difference is probably connected with the inferior acuteness of smell in man, as compared with the lower animals.

The nasal passages are provided with nerves from three sources.

I. The first and most important of these are the *olfactory nerves* (Fig. 129, $_1$). They are derived from the olfactory bulbs, resting on the cribriform plate of the ethmoid bone, through which their filaments penetrate the upper part of the nasal passages. They contain only pale, flattened, nucleated nerve fibres, destitute of a medullary layer. Their branches divide and subdivide, forming microscopic plexuses in the substance of the olfactory membrane; and the finest nervous ramifications have been followed nearly to the epithelial surface of the membrane.

Fig. 129.



Distribution of Nerves in the Nasal Passages.—1. Olfactory bulb, with its nerves. 2. Nasal branch of the fifth pair. 3. Spheno-palatine ganglion.

There is no doubt that the filaments given off from the olfactory bulbs are the special agents for communicating olfactory impressions, and that they are the only ones endowed with this kind of sensibility.

So far as we can judge from the results of experiment, they are not capable of receiving or transmitting any other sensations than those excited by odoriferous substances.

II. The second set of nerves distributed to the nasal passages consists of the *nasal branch of the fifth pair*, and its ramifications (Fig. 129, $_2$). This nerve, after entering the cavity of the nose a little in advance of the cribriform plate of the ethmoid bone, is distributed mainly to the mucous membrane covering the inferior turbinated bone and lining the inferior meatus, which it supplies with general sensibility. Some of its filaments are also continued into the mucous membrane of the olfactory region, in proximity with those of the olfactory nerves; and this region, according to the observations of Babuchin,* possesses consequently a certain amount of general sensibility, though much less than the remainder of the nasal passages.

III. The third set of nerves are derived from the *spheno-palatine ganglion of the sympathetic* (Fig. 129, $_3$), which supply the mucous membrane of the posterior part of the nasal passages and the muscles of the posterior nares. Finally, the muscles of the anterior nares are supplied by filaments of the facial nerve.

Necessary Conditions of the Sense of Smell.—In order to produce an olfactory impression, the emanations of the odoriferous body must be *drawn freely through the nasal passages.* As the olfactory membrane is situated only in the upper part of these passages, whenever a faint or delicate odor is to be perceived, the air is forcibly directed toward the superior turbinated bones, by a peculiar inspiratory movement of the nostrils, very marked in many of the lower animals. As the odoriferous vapors arrive in the upper part of the nasal passages, they are probably dissolved in the secretions of the olfactory membrane, and thus brought into relation with its nerves. Inflammatory disorders interfere with the sense of smell, both by altering the secretions of the part, and by causing tumefaction of the mucous membrane and obstruction of the nasal passages.

A distinction is to be made between true *odors* and the excitement of the general sensibility of the nasal membrane by irritating substances. Some of the odors are similar in their nature to impressions of taste. Thus there are sweet and sour smells, though none corresponding to the alkaline or the bitter tastes. Most odors, however, are of a peculiar nature and difficult to describe; but they are always distinct from the simply irritating properties which belong to certain vapors and gases. Thus, pure alcohol is principally a stimulant to the mucous membrane; but wines have in addition odoriferous qualities, due to ingredients of vegetable origin.

The vapor of pure acetic acid is simply irritating; while vinegar has also a peculiar odor, derived from its vegetable constituents. Ammonia is an irritating gas, but contains no proper odoriferous principle.

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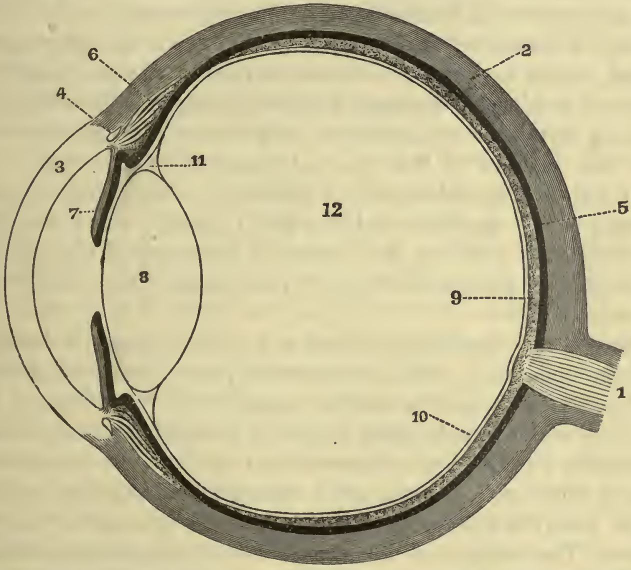
* Stricker's Manual of Histology, Buck's Edition. New York, 1872, p. 799.

The sense of smell, which is only moderately developed in man, is very acute in many animals. The dog will not only discover game and follow it by the scent, but will distinguish individuals by their odor, or recognize articles of dress belonging to them by the minute quantity of odoriferous vapor adhering to the fabric.

Sense of Sight.

This is the most remarkable of all the senses, both for the special nature of its impressions, the complicated structure of its apparatus, and the variety and value of the information which it affords with regard to external objects. It is by this sense that we receive impressions of light and color, with all their modifications of intensity and combination, and acquire our principal ideas of form, space, and movement. The eye is equally sensitive to the impressions of light, whether it come from near or remote objects, or even from the immeasurable distances of the fixed stars. It is superior to the other organs of sense in its rapidity of action, and in the delicacy of the distinctions which it is capable of making in the physical qualities of external objects; and it affords the most continuous and indispensable aid for all the ordinary occupations of life.

Fig. 130.



Horizontal Section of the Right Eyeball.—1. Optic Nerve. 2. Sclerotic coat. 3. Cornea. 4. Canal of Schlemm. 5. Choroid coat. 6. Ciliary muscle. 7. Iris. 8. Crystalline lens. 9. Retina. 10. Hyaloid membrane. 11. Canal of Petit. 12. Vitreous body.

Organ of Vision.—The eyeball consists of a spheroidal fibrous sac, the *sclerotic coat* (Fig. 130, $_2$), filled with fluid and gelatinous material, provided anteriorly with a transparent portion, the *cornea* ($_3$), and lined posteriorly with a nervous expansion, the *retina* ($_9$), which is sensitive to light, and which receives the luminous rays admitted through the cornea. The cavity of the eyeball is therefore like that of a room with but one window, where all the light enters in front, and strikes the back wall of the apartment. There are, in addition to the above-mentioned parts, a transparent refracting body with convex surfaces, the *crystalline lens* ($_8$), by which the light is concentrated at the retina; a perforated muscular diaphragm, the *iris* ($_7$), placed in front of the lens, which regulates the quantity of light admitted through its central orifice, the pupil; and finally a vascular membrane with an opaque layer of blackish-brown pigment, the *choroid* ($_5$), lining the inner surface of the sclerotic and the posterior surface of the iris, thus preventing reflections within the eye, and absorbing the light which has once passed through the retina. The construction of the eyeball, in its general arrangement as an organ of vision, is not unlike that of a photographic camera; where the sensitized plate at the back part represents the retina, the blackened inner surface of the box the choroid, while the optical glasses of the tube in front perform the office of the crystalline lens and cornea of the eyeball.

Sclerotic Coat.—The sclerotic, so named from its toughness and resistance, is the external protective membrane of the eyeball. It is composed of condensed connective tissue, similar to that of the fasciæ and fibrous membranes in general; and toward its anterior third it receives the tendons of the external muscles of the eyeball, which become fused with its substance. Posteriorly it is continuous with the neurilemma of the optic nerve (Fig. 130, $_1$), which penetrates it from behind at its entrance into the eyeball. A portion of the sclerotic is visible anteriorly through the conjunctiva, forming the so-called "white" of the eye.

Cornea.—The cornea, which derives its name from its horny consistency and appearance, forms the anterior part of the wall of the eyeball. It occupies the nearly circular space left at this situation by the deficiency of the sclerotic, with which it is continuous at its edges; the difference in the physical appearance of the two being that the sclerotic is white and opaque, while the cornea is colorless and transparent, so that the colored iris and dark pupil are visible through its substance. The surface of the cornea has a sharper curvature than that of the sclerotic, and projects from the front of the eyeball, like a small dome set upon a larger one. Its outline, where it joins the edge of the sclerotic, is a little oval in form, its transverse diameter being slightly longer than the vertical. At its centre, it is about 0.8 millimetre in thickness, becoming a little thicker at its edges. Its anterior surface is kept polished and brilliant by the watery lachrymal secretion, distributed over it by the movements of the eyeball and lids.

At the outer border of the cornea there is a small circular canal, the *canal of Schlemm* (Fig. 130, $_4$), enclosed in this part of the wall of the eyeball. The posterior wall of the canal of Schlemm is composed of elastic and tendinous tissue, and gives attachment to the ciliary muscle on the one hand, and on the other to the outer border of the iris. The canal is regarded by most anatomists as occupied by a venous plexus, receiving veins from the ciliary muscle and from the anterior part of the sclerotic.

Choroid.—The choroid coat is a vascular and pigmentary membrane, lining the inner surface of the sclerotic, and presenting anteriorly a thickened portion, the "ciliary body." The inner part of the ciliary body is thrown into radiating folds, the "ciliary processes," which surround the borders of the crystalline lens. The inner surface of the choroid is occupied by a layer of hexagonal nucleated cells, filled with blackish-brown pigment. Similar pigment is also deposited, though less abundantly, in the substance and near the external surface of the choroid. At its anterior part, the choroid is separated from the sclerotic by the ciliary muscle (Fig. 130, $_6$). This muscle is composed of unstriped fibres, which arise from the posterior wall of the canal of Schlemm, at the junction of the sclerotic and cornea, and thence diverge in a radiating direction, outward and backward, to be inserted into the external surface of the choroid, where it passes into the folds of the ciliary processes. At the anterior and inner part of the muscle there are also bundles of circular fibres, parallel with the margin of the cornea. The muscle is thus composed of two parts, namely, an internal circular, and an external radiating portion, the fibres of which are more or less interwoven with each other at its inner edge.

Iris.—The iris is a variously colored membrane, extending across the cavity of the eyeball, attached by its external border to the posterior wall of the canal of Schlemm, and presenting at its centre the nearly circular orifice of the pupil. It consists of connective and muscular tissue, with an abundant supply of blood-vessels, and is covered on its posterior surface by a layer of blackish-brown pigment cells, continuous with those of the choroid. The color of the iris, which appears, in different individuals, blue, gray, brown, or black, depends on the abundance and disposition of its pigmentary elements. In gray and blue eyes, the visible hue of the iris comes from the diffused light of its semi-transparent tissues, seen against the dark background of the pigment layer on its posterior surface. In brown and black eyes, the pigment is more abundant, and is deposited, according to Kölliker and Cruveilhier, not only on the posterior aspect of the iris, but also in its stroma, between its fibres, and to some extent even on its anterior surface. It thus predominates, and extinguishes more or less completely the diffused light of the remaining elements of the tissue.

The position of the iris is such that while its outer border is attached to the junction of the cornea and sclerotic, its central portion is in contact with the anterior surface of the crystalline lens. According to Helmholtz,* the iris in myopic eyes is sometimes so nearly flat that it throws no perceptible shadow under an extreme lateral illumination; but in normal eyes, as a rule, the portion immediately surrounding the pupil is sufficiently prominent to throw a distinct shadow; and if the source of illumination be not more than one millimetre in advance of the edge of the cornea, the shadow may extend even to its opposite border.

When the pupil dilates, the central prominence of the iris of course diminishes, or disappears; but, according to Helmholtz, the pupillary border of the iris hardly separates from the anterior face of the lens, even in the most complete dilatation obtainable by belladonna.

The muscular fibres of the iris are arranged in two sets, namely, the sphincter and dilator muscles of the pupil.

The *sphincter pupillæ* is composed of circular fibres, situated at the pupillary margin of the iris, in such a manner that their contraction diminishes the orifice of the pupil, while their relaxation allows its enlargement. When the sphincter is in a state of moderate contraction, the remaining non-contractile tissues are thrown into radiating folds, which extend from the pupillary margin for one-third or one-half the distance toward the outer border of the iris.

The *dilator pupillæ*, which consists of radiating fibres, is more difficult of demonstration, and its existence in man continued to be a matter of uncertainty, after it was known to be present in animals. It has, however, been described by so many independent observers, that there can be no doubt of its forming a normal part of the muscular apparatus of the iris. Its fibres are interwoven with those of the sphincter at the pupillary margin, and thence diverge toward the attached border of the iris, either as isolated bundles running between the blood-vessels (Brücke, Kölliker), or as a very thin, continuous sheet on the posterior surface of the iris, beneath its pigmentary layer (Henle, Iwanoff). According to Kölliker, the iris also contains elements analogous to the fibres of elastic tissue, which may assist in its dilatation.

The pigmentary layer, which is continuous, over the inner surface of the choroid, the ciliary processes, and the posterior surface of the iris, is called the system of the *uvea*, from its resemblance to the skin of a purple grape separated from its stem, the opening of the membranous sac at the point of detachment representing the orifice of the pupil. Owing to the existence of this layer, no light can penetrate the eyeball except through the pupil; and rays which have reached the retina at any point are arrested there, and prevented from dispersion over other parts.

Aqueous Humor and Vitreous Body.—The cavity of the eyeball is divided, by the transverse partition of the iris, into two portions—an anterior and posterior. The portion in front of the iris, called the "anterior chamber," is filled with a colorless, transparent watery fluid, the *aqueous humor*. This fluid serves to maintain the internal tension of the eyeball, and to allow of changes in the iris and crystalline lens,

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* Optique Physiologique. Paris, 1867, p. 20.

without affecting the external configuration of the cornea. The posterior and larger portion of the cavity of the eyeball is filled by a semi-fluid gelatinous substance, *the vitreous body*, so called from its transparent and glassy appearance. Its refractive power, according to Helmholtz, though slightly greater than that of the aqueous humor, does not differ much from that of water. It distends the greater part of the cavity of the sclerotic, supports the retina which lies upon its surface, and preserves the spheroidal form of the eyeball.

The vitreous body is enveloped by an exceedingly thin, colorless membrane, for the most part without definite structure, and according to Kölliker, not more than 4 mmm. in thickness. This is the "hyaloid membrane" (Fig. 130, $_{10}$). It extends over the posterior and middle portions of the vitreous body to a zone corresponding with the ciliary body of the choroid. Here it becomes thicker and divides into two layers. The anterior layer, which is the stronger of the two, the *zone of Zinn*, extends forward and inward, remaining adherent to the ciliary body, and terminates in the capsule of the crystalline lens, just in front of its lateral border. The posterior layer passes inward and a little backward, terminating also in the capsule of the lens, but a little behind its lateral border. The triangular canal between the two layers of the hyaloid membrane and the lateral border of the lens is the *canal of Petit* (Fig. 130, $_{11}$), and is filled with a transparent serosity. The lens is thus suspended, from all sides, by a double layer derived from the hyaloid membrane.

Crystalline Lens.—The lens is a transparent, refractive body, with convex anterior and posterior surfaces, placed directly behind the pupil, where it is retained in position by the counterbalancing pressure of the aqueous humor and the vitreous body, and by the suspensory layers of the hyaloid membrane.

As its refractive power is greater than that of the cornea or the aqueous humor, it acts, by virtue of its double-convex form, as a converging lens, to change the direction of rays passing through it, and bring them to a focus behind its posterior surface. The amount of convergence thus effected by a refractive lens depends on the substance of which it is composed and the curvature of its surfaces. The stronger the curvatures, for lenses composed of the same material, the greater their refractive power for luminous rays. In the crystalline lens of the human eye, the two surfaces are different in curvature; the anterior being comparatively flat, the posterior more convex. According to the estimates of Listing, based on a variety of measurements and adopted by Helmholtz, the radius of curvature for the anterior surface is, on the average, 10 millimetres, that for the posterior surface 6 millimetres.

This makes the crystalline lens the strongest refracting body in the eyeball, and by its aid parallel or diverging rays are brought to a focus at the retina. This effect is not due entirely to the lens, since the convex form of the cornea and the more or less spheroidal figure of the whole eyeball have in some degree a similar action. According to

Helmholtz, parallel rays would be brought to a focus by the cornea alone at a point 10 millimetres behind the retina. But on passing through the lens, their convergence is increased to such a degree that they are concentrated at the retina.

The function of the crystalline lens is to give perception of form and outline. If the eye consisted only of a sensitive retina, covered with transparent integument, although impressions of light would be received by such a retina, they could give no idea of the form of objects, but only the sensation of a confused luminosity. This condition is illustrated in Fig. 131, where the arrow, *a*, *b*, represents the luminous object, and the vertical dotted line, at the right of the diagram, represents the retina. The rays diverging from every point of the object will thus reach every part of the retina (1, 2, 3, 4,); and each one of these parts will receive rays coming both from the point of the arrow, *a*, and from its butt, *b*. There will, therefore, be no distinction, upon the retina, between different parts of the object, and no perception of its figure. But if, between the object and the retina, there be inserted a lens, with the proper curvatures and density, as in Fig. 132, the effect will be different. All the rays emanating from *a* will then be concentrated at *x*, and all those emanating from *b* will be concentrated at *y*. Thus the retina will receive the impression of the point of the arrow separate from that of its butt; and all parts of the object, in like manner, will be distinctly perceived.

Fig. 131.

Vision without a Lens.

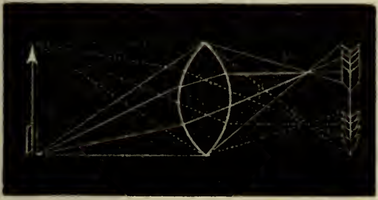
Fig. 132.

Vision with a Lens.

The action of a lens, in thus focussing luminous rays at a particular point, may be illustrated in the following manner: If a sheet of white paper be held at a short distance from a candle flame, in a room with no other source of light, the whole of the paper will be moderately and uniformly illuminated by the diverging rays. But if a double convex glass lens, with suitable curvatures, be interposed between the paper and the light, the outer portions of the paper will become darker and its central portion brighter, because a portion of the rays are diverted from their original course and bent inward. By varying the distance of the lens from the paper, a point will at last be found, where none of the light reaches the external parts of the sheet, but all of it is concentrated upon a single spot; and at this spot will be seen a distinct image of the end of the candle and its flame.

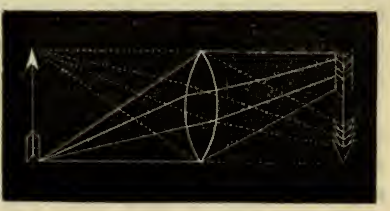
Perception of the figure of external objects therefore depends on the action of the crystalline lens in converging all the rays, emanating from a given point, to a focus at the retina. For this purpose, the density of the lens, the curvature of its surfaces, and its distance from the retina, must all be properly adapted to each other. If the lens were too convex, and its refractive power excessive, or if its distance from the retina were too great, the rays would cross each other and become partially dispersed before reaching the retina, as in Fig. 133. The visual impression, therefore, of any point in the object, would not be concentrated and distinct, but diffused and dim, from being more or less dispersed over the retina, and interfering with the impressions from other parts. On the other hand, if the lens were too flat, as in Fig. 134, or too near the retina, the rays would not come to a focus, but would strike the retina separately, producing a confused image, as before. In both cases, the immediate cause of the confusion of sight would be the same, namely, that rays from each point of the object are dispersed over the retina; but in the first instance, this is because they have converged and crossed each other; in the second, it is because they have only approximated, and have never come to a focus.

Fig. 133.



Indistinct Image from excessive refraction.

Fig. 134.



Indistinct Image from deficient refraction.

The proof that the rays are thus concentrated, in the living eye, at the retina, is furnished by the ophthalmoscope. This instrument consists of a mirror, so placed as to illuminate by reflected light, through the pupil, the bottom of the eye under observation, and perforated at its centre by a small opening through which the observer looks. By this means the retina and its vessels, as well as the images delineated upon it, may be seen. According to Helmholtz, luminous objects at a certain distance, when distinctly perceived by the person under observation, present to the eye of the observer well-defined inverted images upon the retina. Furthermore, if, from the eyeball of a recently-killed animal, a circular portion of the sclerotic and choroid be removed at its posterior part, similar inverted images of objects in front of the cornea may be seen by transparency on the exposed portion of the retina.

It is accordingly certain that divergent luminous rays, in passing through the eyeball, are brought to a focus at the retina, principally by means of the crystalline lens. The formation of a visible image at this spot does not by itself explain the phenomena of vision, since these images are not seen by the individual, and we should not even know of their existence except for the results of experiment and observation. But it shows that all the light coming from each part of the object is made to fall upon a single point of the retina; and it thus becomes possible to perceive the figure of an object, as well as its luminosity.

Retina.—The retina is the most essential part of the organ of vision, since it is the only one directly sensitive to light. It forms a nearly transparent membrane, composed of nervous elements, situated between the inner surface of the choroid and the outer surface of the hyaloid membrane, and extending from the entrance of the optic nerve to the commencement of the ciliary body. Here it terminates by an indented border, the *ora serrata*, nearly at the plane of the posterior surface of the crystalline lens. In front of this region it is replaced by an attenuated layer, in contact with the surface of the ciliary body, which contains no nervous elements. It has, accordingly, the form of a membrane moulded upon a nearly hemispherical surface, with its concavity directed forward, and receiving the rays admitted through the pupil. Its greatest thickness is in the immediate vicinity of the optic nerve, where it measures, according to Kölliker, 0.40 millimetre. At a short distance from this point it is reduced to 0.20, and thence becomes gradually thinner in its middle and anterior portions. At the ora serrata, it is only 0.09 millimetre in thickness.

The retina consists of superimposed layers, containing many different microscopic elements. In regard to its physiological properties, so far as they have been determined, four of these layers may be distinguished as representing its essential constituents. These layers, counting from the inner to the outer surface of the retina, are as follows: 1. The layer of nerve fibres; 2. The ganglionic layer of nerve cells; 3. The layer of nuclei; 4. The layer of rods and cones.

1. *Layer of Nerve Fibres.*—The optic nerve joins the posterior part of the eyeball about 2 millimetres inside its longitudinal axis, and at a slightly lower horizontal plane. Its neurilemma becomes continuous with the sclerotic coat, while its nerve fibres penetrate the cavity of the eyeball. Up to this point the optic nerve consists of dark-bordered medullated fibres, having, according to Kölliker, a diameter of from 1 to 4.5 mmm. But at their entrance into the eyeball they become much smaller, being reduced, on the average, to less than 2 mmm., and many of them to less than 1 mmm. in diameter. Owing to these changes, the nerve appears suddenly diminished in size at its passage through the sclerotic. Internally it forms a slight prominence at the fundus of the eye, the so-called *papilla;* and the central artery and vein of the retina emerge at this point. From the papilla as a centre the optic nerve fibres, which have thus reached the inner surface of the retina, radiate laterally in every direction under the form of a closely set layer. This layer diminishes gradually in thickness from the centre outward, owing to the fact that its fibres terminate successively in the deeper

parts of the membrane. The longest fibres continue their course to the ora serrata, beyond which none are visible.

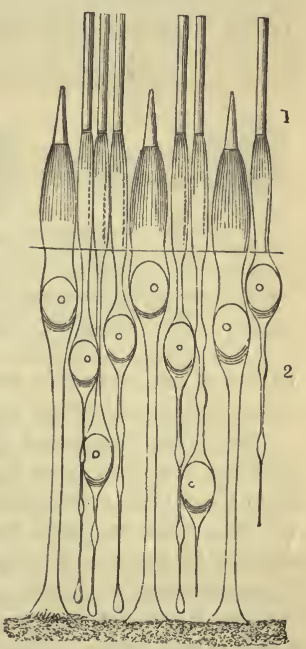
2. *Ganglionic Layer of Nerve Cells.*—This layer, which is situated immediately outside the former, contains multipolar nerve cells, similar to those of the gray substance of the brain. According to Kölliker, they vary in size from 9 to 36 mmm. in diameter, and are provided with pale, ramified prolongations. Some of these prolongations are directed toward the more external portions of the retina; others pass in a horizontal direction, and, according to some observers (Kölliker, Müller, Corti), become continuous with optic nerve fibres.

3. *Layer of Nuclei.*—The most characteristic elements of this layer have, in the main, the aspect of nuclei; although by some observers (Kölliker, Schultze), they are regarded as nucleated cells, in which the enveloping cell-substance is scanty, as compared with the size of the nucleus. The nuclei, sometimes called "grains" or "granules," are oval bodies, with their long axes perpendicular to the surface of the retina. They are of two varieties, differing mainly in size; the larger being from 9 to 13 mmm. in length, the smaller one-half or two-thirds as long. They are all contained in varicose enlargements of slender fibres, also directed perpendicularly to the surface of the retina, and extending through the whole thickness of the layer. These are presumed to be of the nature of nerve fibres, and to represent, directly or indirectly, the continuations of those from the optic nerve. At their outer extremities they are continuous with the elements of the following layer.

4. *Layer of Rods and Cones.*—This is the most remarkable of the retinal layers, consisting of elements more peculiar in form than those found elsewhere, and most directly connected with the physiology of luminous impressions. As their name indicates, these elements are of two kinds, namely, the "rods" and the "cones." There is reason to believe that they are modifications of each other, and that their offices in vision are essentially similar.

The *rods* (Fig. 135) are straight, elongated, cylindrical bodies, composed of a transparent, homogeneous substance, remarkable for its highly refractive power. They are about 50 mmm. in length by a little less than 2 mmm. in diameter. They are placed parallel with each other, closely packed side by side, perpendicularly to the surface of the retina. At its outer extremity each rod terminates by

FIG. 135.



DIAGRAMMATIC SECTION, from the posterior portion of the human retina.—1. Layer of rods and cones. 2. Layer of nuclei. (Schultze.)

a plane; at its inner extremity it tapers to a point and becomes continuous with a fibre of the preceding layer. According to Schultze, the inner half of each rod is slightly thicker, and exhibits rather less refractive power than the outer half.

The *cones* differ from the rods mainly in their tapering form and the greater diameter of their inner portion, which is generally two or three times as thick as that of the rods. Their extremities, in some regions, stop short of the outer surface of the retina, as in Fig. 135, while in that of most perfect vision they reach the same level with the rods. Each cone is connected at its inner extremity with a nucleated fibre of the preceding layer, the only peculiarity in this respect being that the fibres and nuclei connected with the cones are larger than those connected with the rods.

Over the greater part of the retina the rods are more abundant than the cones. When viewed from the outer surface (Fig. 136, *A*), their closely packed extremities present the appearance of a fine mosaic, while the cones are interspersed among them in smaller numbers. At the borders of the macula lutea, the cones are more abundant, being only separated from each other by single ranges of rods (*B*); and at its central portion (*C*) there are only cones, the rods being entirely absent. But the cones at this point are longer and more slender than elsewhere. In the following figure the smaller circles represent the rods, the larger circles the cones; and in the interior of each cone is seen a section of its conical extremity.

Fig. 136.

Outer Surface of the Retina, showing the ends of the rods and cones.—*A*. From the lateral portion of the eyeball. *B*. From the edge of the macula lutea. *C*. From the macula lutea. (Helmholtz.)

Reception of Luminous Impressions by the Retina.—It appears, from the above, that the retina is not simply an expansion of the optic nerve. It is an apparatus of special structure, adapted for the reception of luminous rays, and connected by the optic fibres with the central parts of the brain. An examination of the manner in which impressions of light are received brings into view the following facts:

The Optic Nerve and its Fibres are insensible to light.—Notwithstanding that this nerve is capable of transmitting impressions of sight from the retina to the brain, yet in order to do this, it must first receive its own stimulus from the retina. Its fibres cannot be called into activity by the direct influence of luminous rays. This is shown by the experiment of Donders, in which a light of some intensity is concentrated upon the optic nerve, without being allowed to reach the tissue of the retina. When the bottom of the eye is illuminated by the ophthalmoscope, the observer sees the general surface of the retina of a red or brownish color, while the papilla, at the entrance of the optic nerve, presents itself as a circular white spot. This spot is occupied entirely by optic nerve fibres, the elements of the retina commencing only beyond its borders. If the light of a candle flame at some distance be thrown upon the retina, it is perceived by the person under observation, as well as its image by the observer. If the eye, however, be turned in such a direction as to bring the image of the flame upon the white circle of the papilla, this circle, and the nerve fibres of which it is composed, are visibly illuminated to a certain depth, owing to the translucency of their substance; but the light is no longer perceived by the person under examination. The moment the image is allowed to pass beyond the limits of the white circle, its light becomes perceptible.

The Blind Spot.—The region, accordingly, occupied by the entrance of the optic nerve, from which the proper elements of the retina are absent, is a blind spot, where luminous rays make no perceptible impression. The diameter of this spot, according to the average measurements by Listing, Hannover, and Helmholtz, is 1.65 millimetre, and it covers in the field of vision a space of about 6 degrees. Notwithstanding its existence, no dark point is usually observed in the field of vision, for the following reasons: The blind spot is not situated in the visual axis of the eye, but corresponds with the entrance of the optic nerve, nearer the median line (Fig. 130). Consequently the image of an object in the normal line of vision cannot fall upon this spot, but is always outside of it, in the visual axis. Even an object perceived outside the direct line of sight can never reach the blind spot of both eyes at once. If so placed that its image falls on the blind spot of one eye, it will necessarily reach the retina of the other eye at a different point, and will thus be perceived. But if one eye alone be employed, there is always a small portion of the field of vision which is imperceptible. This deficiency is not generally noticed, because it is in a part of the field to which our attention is not directed, and where the distinction of objects, under moderate illumination, is so imperfect, that the momentary absence of one is not regarded. It may, however, be made apparent by using for the test a single strongly defined object, like a white spot on a black ground, the presence or absence of which may be observable, even in indirect vision.

If the left eye be covered and the right eye directed steadily at the white cross in Fig. 137, the circular spot will also be visible, though less distinctly, since it will be out of the direct line of sight. Let the page be held vertically at the height of the eyes, and at a convenient distance for seeing both objects in the above manner. If it be now moved slowly backward and forward, a point will be found where the circular spot disappears, because its image has fallen upon the blind spot; while both within and beyond this distance it is again visible. It may also be made to reappear by inclining the page laterally to the right or left; since this brings its image either above or below the blind spot.

The experiment may be varied by fixing two cards, at the height of the eyes, upon a dark wall, two feet apart from each other. If the left eye be covered, and the right eye fixed upon the left-hand card, the other will disappear from view at a distance of about eight feet from the wall.

It is evident, furthermore, that the optic nerve fibres are not directly sensitive to light, even outside the blind spot. These fibres radiate from the entrance of the optic nerve, forming a continuous sheet on the inner surface of the retina; terminating at successive points in the retinal membrane to its extreme border. A luminous ray striking the retina near the fundus of the eye must, therefore, traverse a considerable number of nerve fibres, connected at their peripheral extremities with different parts of the retina; and, though coming from a single point, it would thus cause the sensation of an extended line. As distinct points are separately perceived, although the rays emanating from each have passed through the whole layer of nerve fibres in the retina, it follows that these fibres are not directly affected by the action of light.

Fig. 137.

Diagram, for observing the situation of the blind spot. (Helmholtz.)

The sensitive elements of the retina are in its posterior or external layers.—This is apparent partly from the phenomena observed when the retinal blood-vessels are made visible within the eye. These vessels and their branches radiate from the entrance of the optic nerve. Their ramifications, down to a certain size, are situated in the innermost layer of the retina, and it is only the finest subdivisions which pass into the layer of ganglionic cells. The two outer layers, namely, that of the nuclei, and that of the rods and cones, are destitute of blood-vessels. Owing to this arrangement, the outer layers of the retina, situated behind the main branches of the blood-vessels, lie in the shadow of these branches, since the light comes directly from the front through the pupil. The shadows thus thrown are not usually perceived, because the portions of retina covered by them are habitually in shadow at the same points, and their sensibility to light is greater in proportion. But they may be rendered perceptible by throwing them, under oblique illumination, upon unaccustomed points of the retina.

Let a lighted candle be held, in a dark room, about three inches from the outer angle of the eye, and about 45 degrees in front of the plane of the iris. On moving the candle alternately up and down, the field of vision becomes filled with an abundant tracery of arborescent figures, the counterpart of the retinal blood-vessels. The form of the vessels is marked in purple-black, on a finely granular grayish-red ground. The point of entrance of the vascular trunks may be seen, with their two principal branches passing respectively upward and downward, and breaking into ramifications of various curvilinear form. If the candle be held motionless, the figures rapidly fade, since they are only visible from the contrasts made by the shadows falling in succession on different parts of the retina.

As the blood-vessels of the retina are situated nearly at its anterior surface, the motion of their shadows, perceptible on varying the position of the light, gives a means of ascertaining how far behind this surface the sensitive elements are situated. According to Müller,* this distance must be, in various cases, from 0.17 to 0.36 millimetre; and the same observer finds the posterior layers of the retina distant from its anterior surface from 0.20 to 0.30 millimetre. It is, therefore, one or both of the posterior layers, namely, the rods and cones, and the nuclei immediately beneath, in which luminous rays produce their effect.

Macula Lutea and Point of Distinct Vision.—The macula lutea, or yellow spot of the retina, is an oval space, about 2 millimetres in transverse diameter, between 2 and 2.5 millimetres outside the entrance of the optic nerve. According to Helmholtz, it is placed a very little beyond the middle of the fundus of the eyeball, toward its temporal side. It is distinguished from the remainder of the retina by its yellow tinge, due to the presence of an organic pigment.

At its centre is a minute depression, the *fovea centralis*, where, owing to its steeply sloping sides, the thickness of the retina is reduced, at its deepest part, to less than one-half. Its position in the macula lutea, in ophthalmoscopic examinations, is marked by a peculiar colorless reflection. The macula lutea, and especially the fovea centralis, *is the point of most distinct vision*, where the image of an object, in the direct line of sight, falls upon the retina. According to the observations of Donders, confirmed by Helmholtz, if, while the retina is illuminated by the ophthalmoscope, the person under observation fixes the eye upon several different objects in succession, the minute reflection which marks the fovea centralis always places itself upon the optical image of the object fixed by the eye; and this appearance is so constant that the observer can tell with certainty, from the place occupied by the reflection, at what object the sight is directed.

The importance of the macula lutea and fovea centralis, in the exercise of vision, gives a special interest to the anatomy of this part of the retina; and microscopic researches have shown that it presents

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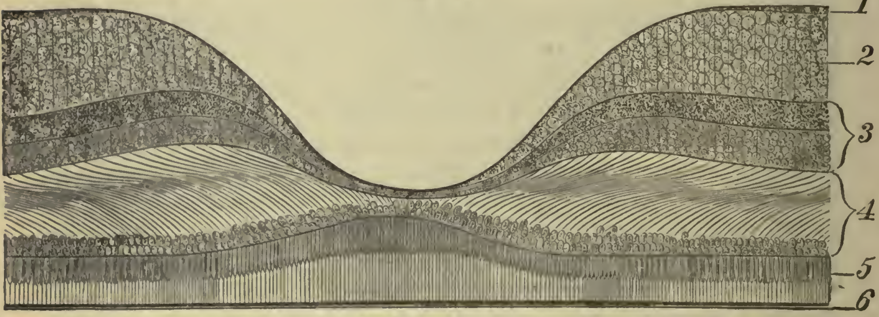
*In Helmholtz, Optique Physiologique. Paris, 1867, p. 289.

peculiarities of structure corresponding with its physiological endowments.

The macula lutea is distinguished, in the first place, by the *absence of the layer of nerve fibres.* Those fibres, according to Kölliker, which, in radiating from the entrance of the optic nerve, reach the edges of the macula, lose themselves among the nerve cells of its ganglionic layer. The others curve round its borders on each side, and resume their peripheral course beyond; so that there are none to be found within the limits of the yellow spot.

Secondly, the nerve cells of the ganglionic layer are more abundant in the macula lutea than elsewhere. Over the greater portion of the retina, according to Schultze, these cells are arranged in a single plane; but in the yellow spot they form several superimposed ranges. Toward the centre of the yellow spot, on the other hand, they diminish in number, and are entirely wanting at the fovea centralis.

Fig. 138.



Diagrammatic Section of Human Retina, through the macula lutea and fovea centralis.—1. Inner surface of the retina. 2. Ganglionic layer of nerve cells. 3. Intermediate layers of the retina, disappearing at the centre of the macula lutea. 4. Layer of nuclei, showing the oblique course of its fibres in this region. 5. Layer of rods and cones; consisting at its central portion exclusively of attenuated and elongated cones. 6. Outer surface of the retina. The depression in the middle of the diagram is the fovea centralis. (Schultze.)

Thirdly, owing to these modifications, the retina, at the fovea centralis, *consists only of its two external layers*, namely, the layer of nuclei and the layer of rods and cones. Even these layers exhibit, at the same point, important peculiarities in the form and arrangement of their elements.

In the layer of nuclei, the fibres with which they are connected, instead of remaining perpendicular to the surface of the retina, bend obliquely outward, to reach its more superficial parts in the outer portions, or beyond the borders, of the yellow spot. Thus the layer is much diminished in thickness, though still containing nuclei, connected, by their usual extensions, with other parts of the retina.

Finally, the layer of rods and cones, at the macula lutea and fovea, is distinguished by special features from the corresponding parts elsewhere. At this situation it is increased in thickness, and consists exclusively of slender elongated cones. The diameter of the cones at their base is reduced from 6 mmm. to 3 or 3.5 mmm.; while their length reaches 100 mmm., or about double what it is elsewhere. Each cone is connected, through the nucleus and fibre of the preceding layer, with other portions of the retina, and, no doubt, in some way, with the nerve fibres of its inner layer.

Thus, the perception of light is a process consisting of several successive acts. The luminous ray passes through the tissue of the retina, until it reaches the layer of rods and cones. In these elements it produces a reaction of whose nature we are ignorant. It might be compared with that caused by the same agent in the sensitive film of a photographic camera; but this comparison would be only one of analogy, and would not imply any identity of molecular action in the two cases. It would simply express the fact, which is undoubtedly established, that the luminous ray, after traversing all the other transparent and refracting media of the eye without leaving any trace of its passage, on arriving at the outer layers of the retina, excites in them a change of condition which is the first step in the visual process. The excitement of the retina then calls into activity the fibres of the optic nerve, which in turn transmit the stimulus to their origin at the base of the brain. Thus far, there is no conscious perception, nor even any nervous effect resembling our idea of luminosity. The retina is distinguished from other nervous tissues by being sensitive to light; that is, it may be thrown into a state of activity under the influence of a luminous ray. But it has no proper *perception* of light, any more than the silvered film of a photographic plate; and, if the optic nerve be severed, blindness results, however perfect the condition of the retina.

On the other hand, the optic nerve fibres, which are insensible to the direct action of light, are thrown into excitement by the condition of the retinal tissue. There is no reason for believing that the optic fibres are different in kind from those of other sensitive nerves. Their office is simply that of transmitting a stimulus from and to certain special structures containing nerve cells. By the optic nerve fibres the stimulus is received from the retina and communicated to the brain; and the nervous centres, when thus excited, first produce the sensation and perception of *light*.

Acuteness of Vision in the Retina.—The acuteness of vision, in the retina, is measured by the distance between two visual rays at which they can be perceived as distinct points. If the rays, coming respectively from the top and bottom of an object, are so closely approximated at the retina that the two impressions are confounded, there can be no distinct perception of its figure or dimensions. On the other hand, if the sensibility of the retina be such that the two impressions are separately perceived, the form of the object will be recognized as well as its luminosity, notwithstanding the small size of its retinal image. The figure of a man, six feet high, seen at a distance of ten yards, makes at the cornea a visual angle of 11° 30′, and forms upon the retina an image less than half a millimetre ($\frac{1}{50}$ of an inch) in length;

and yet an abundance of details are distinctly perceptible within this space. The extreme limit of approximation at which two points may be distinguished from each other has been examined by the observation of fixed stars, and by that of parallel threads of the spider's web, or of fine wires, placed at known distances from each other.* These examinations show that, for average well-formed eyes, the smallest visual angle, at which adjacent points can be distinguished, is from 60 to 73 seconds; corresponding to a distance upon the retina of from 4 to 5 mmm. According to Schultze, the diameter of the retinal cones, at the fovea centralis, is from 3 to 3.5 mmm.; and if two beams of light were separated at the retina by a less distance than this, they might fall upon the same cone, and consequently excite the same connecting fibre in the adjacent layer. If the diameter of the cones be the element which determines the acuteness of vision, two luminous points, to be distinctly perceptible, must be separated upon the retina by a distance of at least 3 mmm., and must have a visual angle with each other of at least 42 seconds. In astronomical observations, it is found that two stars can never be separately distinguished by the eye, unless their angular distance from each other is equal to 30 seconds; and very seldom, unless it be as great as 60 seconds. These measurements are hardly sufficient to decide the question; since there has never been an opportunity of examining the size of the retinal elements in an eye, of which the acuteness of vision had been previously tested. But they are enough to indicate a probable connection between the minute structure of the retina and the limit of its sensibility to separate impressions.

The Retinal Red and its alteration by light.—The retina, as usually extracted from the eye of a recently killed animal, is colorless or slightly opaline. But in its normal condition in the living eye, or if extracted without exposure to light, it is of a purple-red hue, due to a transparent coloring matter in its external or posterior layer. This color, the so-called "retinal red," first discovered by Boll,† has been more fully investigated by Kühne.‡ It is seated exclusively in the *rods* of the retina, and is consequently most distinctly marked where these elements are most abundant. The cones, on the other hand, are colorless. At the macula lutea, accordingly, where the cones preponderate over the rods, the reddish tint disappears; and it is entirely absent at the fovea centralis, where the membrane consists only of cones and their appendages. Elsewhere, it extends over the retina to within three or four millimetres of the ora serrata, where it terminates by a tolerably well-defined limit.

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* Helmholtz, Optique Physiologique. Paris, 1867, p. 292.

† Monatsberichte der königliche Preussischen Akademie der Wissenschaften. Jahre 1876. Berlin, 1877, p. 783.

‡ Untersuchungen aus dem Physiologischen Institute. Heidelberg, 1877. Heft 1, 2, 3.

The most striking character of the retinal red is that it is *destroyed by the action of light.* On this account its existence remained long unknown. When the retina is extracted from the eye of an animal in the ordinary way, its exposure during the necessary manipulations is usually sufficient to bleach its color and reduce it to the condition of a grayish or opalescent membrane. In order to obtain it with its normal hue, the animal should be kept in the dark for a short time previous to death; and the eyeball taken out and the retina extracted by the light of a sodium flame, which has comparatively little effect upon its color. If such a retina be exposed to bright daylight its purple-red tint, at first distinctly visible, is destroyed, according to Kühne, in about half a minute. Under a dim daylight it lasts longer, and by ordinary gaslight may continue visible for 20 or 30 minutes; while in a chamber lighted by the sodium flame, or in the dark, it remains for 24 or 48 hours, even after the tissues have lost their freshness and consistency.

By this means the existence of the retinal red has been demonstrated in the rabbit, dog, ox, ape, and badger, in the owl and falcon, in the frog, triton, toad, and salamander, and in several species of fish. In three instances Kühne found it in the human eye, extirpated in the dark or in a sodium-lighted chamber, from subjects who had been protected from the light for a certain time before death.

The retinal red is also destroyed by the action of light during life. This is not usually observable in an eye extracted with the above-mentioned precautions, for the reason that during life the color is regenerated nearly as fast as it is destroyed. Thus a living eye, under moderate illumination, maintains the normal hue of its retina by the constant reproduction of its coloring matter. But if long exposed to light of considerable intensity it may become completely bleached, though its color will be restored by repose in a darkened place. Kühne found that in frogs exposed to daylight, in a glass vessel with a white bottom, the retina becomes bleached after several hours; and that in direct sunshine 15 minutes are sufficient to produce the same effect. But if the animals be then kept in the dark, and examined at various intervals, the color of the retina again begins to be perceptible in about 30 minutes, and is completely restored at the end of an hour and a half.

The source from which the color is thus reproduced is the *choroidal epithelium*, with which the retina lies in contact. If separated from its attachment and exposed to daylight, its color disappears, as already shown, in from 30 seconds to several minutes. But if allowed to remain in the eyeball under a similar exposure, and then extracted under the light of a sodium flame, on bringing it into ordinary daylight it is at first of a deep red. In Kühne's experiments, a portion of a frog's retina, separated from the choroid in daylight until quite bleached, then replaced and allowed to remain in position in the dark for a short time, exhibited, when finally removed, its normal red color. It is accordingly evident that the regeneration of the color does not depend on the circulating blood, since it will take place in the extirpated eyeball; but is affected by the aid of the choroidal epithelium.

The coloring matter of the retina is soluble in *purified bile*, or in *watery solutions of the biliary salts*, and has been extracted by Kühne in this way under the form of a transparent solution. The freshly-extracted frog's retina is macerated from one to two hours in one cubic centimetre of a five per cent. watery solution of the biliary salts. It is then replaced, in the same solution, by another retina, also freshly prepared; and so on until 20 or 30 retinas have been employed for the purpose. The mixture is then filtered and the filtrate allowed to stand until the pigment granules mingled with it have subsided to the bottom, after which the supernatant liquid is removed by a pipette. It forms a clear solution of a carmine-red color. By concentration it assumes a more violet tinge, and if diluted becomes rose-red or pale lilac, according to the amount of dilution.

Solutions of the retinal red are bleached by light, in the same manner as the retina itself. Their color changes, under these circumstances, first to a clear red, then becoming orange, then yellowish, and lastly they are entirely decolorized. Similar changes are effected in the dark by an elevated temperature; beginning at 50° or 52° C., becoming more rapid as the temperature rises, and taking place almost instantaneously from 70° to 74° C.

The local bleaching of the retina under concentrated illumination makes it possible to obtain retinal *optograms*, that is, colorless images of brilliant objects which have been placed before the eye, surrounded by the purple-red hue of the remaining retina. The first result of this kind was obtained by Kühne in the following manner: The fresh retina of a rabbit, extracted under the light of a sodium flame, was spread out on a glass plate and secured by a thin cover-glass on which were several strips of tinfoil, each about one millimetre in width. In this condition it was exposed to light until the bleaching process was complete; and on removing the cover-glass, bands of unchanged purple-red were visible in the retina, wherever it had been protected by the tinfoil. As the form of any luminous object in front of the eye is concentrated upon a single part of the retina, this part will be bleached, if the exposure be sufficient, while the remaining portions retain their color, thus presenting a positive image of the luminous object. The method adopted by Kühne for obtaining optograms in the rabbit's or ox's eye is as follows: The eyeball is taken out in a dark chamber with the aid of the sodium flame, and fixed, with the cornea upward, in a blackened box or cylinder, the cover of which is removable. The box containing the eyeball is then placed upon a table directly beneath an illuminated skylight of ground glass, at about four metres' vertical distance, and the cover removed. After an exposure of from one to twenty minutes, according to the intensity of the daylight, the opaque cover is replaced, the eyeball opened in the dark chamber by an equatorial incision, its posterior half freed from the vitreous humor, and placed for twenty-four hours in a four per cent. watery solution of potassium-alum. The last operation is for the purpose of giving to the retina a greater consistency, so that it may be removed from the eyeball without laceration. When the hardening is complete the retina is removed, and placed, with its posterior surface uppermost, upon a porcelain capsule of suitable convexity; when the images of the window-panes are seen in white, with the intervening bars and the surrounding spaces purple-red. On exposure to daylight the images disappear, owing to the bleaching of the whole retina; but if, while still in the dark chamber, it be thoroughly desiccated, its color becomes comparatively indestructible, and the optograms remain visible in daylight for many hours.

Notwithstanding the evident importance of the retinal red, and its sensibility to the influence of light, *it is not immediately essential to the act of vision.* This is manifest, in the first place, from the fact that, in the human eye, it is absent from the macula lutea and fovea centralis; that is, from the spot of greatest retinal sensibility and most distinct vision. Kühne has furthermore demonstrated that frogs whose retinas have been completely bleached by continued exposure to direct sunshine are still capable of vision. Under these circumstances the retinal red is regenerated, even in the dark, somewhat slowly, and does not begin to show itself under half an hour (page 535). During this period, therefore, the animals have no appreciable red in the retinal tissue; and yet they quickly distinguish moving objects, and can even capture flies in their usual manner with readiness and precision. They also show a capacity for distinguishing colors, and in both these particulars exhibit a marked contrast with frogs which have been blinded by extirpation of the eyeballs.

It is accordingly quite uncertain in what way the coloring matter of the retina is subservient to sight. It may be supposed that by its transformation under the influence of light it supplies some material for the continued nutrition of the nervous elements; and that this secondary material is in turn consumed during the act of vision. But so far as our present knowledge extends, there is no satisfactory evidence in regard to its mode of action.

Physiological Conditions of the Sense of Sight.—The eye, so far as regards its physical structure, is an optical instrument, composed of transparent and refracting media, a perforated diaphragm, and a dark chamber, all of which act upon luminous rays according to the same laws as the corresponding parts in a telescope or a camera; and the accuracy of their adjustment is one of the first requisites for the exercise of sight. The eye is also movable in various directions; and certain of its internal parts are under the control of muscular tissues, which contribute to its action. It is furthermore a double organ; and impressions may be acquired by the use of both eyes which cannot be received from one alone. Finally, the sensibility of its nervous elements is liable to modifications, which influence the nature and intensity of the sensations produced. The principal conditions regulating the sense of sight are the following:

Field of Vision.—As the eyeball is placed in the orbit with the cornea and pupil directed forward, there is, in front of each eye, a circular space within which objects are perceptible; while beyond its borders nothing can be seen. This space is the "field of vision." Its extreme limit, in man, reaches nearly 180 degrees of angular distance; that is to say, the light from a brilliant object may be perceived, when the object is in a lateral position, almost as far back as the plane of the iris. The possibility for a ray of light from this source, to penetrate the pupil and reach the retina, depends on the refractive power of the cornea and the curvature of its anterior surface, by which the ray is bent inward and enabled to enter the pupil in an oblique direction. In many animals, where the eyes are more prominent than in man, and the curvatures of the cornea and crystalline lens more pronounced, the field of vision is enlarged in a corresponding degree. In birds and fishes, it is still further modified by the lateral position of the eyes. The ostrich, with the head directed forward, can easily see objects a few yards behind its back; and in many fish, when examined from different points in an aquarium, it is impossible for the observer to place himself in any position, above, behind, or on either side, where he cannot see one or both of the pupils of the animal. The field of vision consequently, for such animals, is a complete sphere; the light being perceptible from every point of the surrounding space. In man, the outer borders of the field of vision are ill defined; and objects at a lateral distance of 90 degrees must be very brilliant to attract attention. For practical purposes, the space within which objects are perceptible is not more than 75 degrees on each side, or 150 degrees for the entire field of vision.

Line of Direct Vision.—Within the field of vision there is only one point, at its centre, where objects can be perceived with distinctness; and the prolongation of this point, in the visual axis, is called the "line of direct vision." Objects upon this line can be distinctly seen; all others, situated on either side, above or below it, are perceived only in an imperfect manner. If the observer place himself in front of a row of vertical stakes, he can see those directly before the eye with perfect distinctness; but those on either side appear as uncertain and confused images. On looking at the middle of a printed page, in the line of direct vision, we see the distinct outlines of the letters; while at successive distances from this point, the eye remaining fixed, we distinguish first only the separate letters with confused outlines, then only the words, and lastly only the lines and spaces.

This limitation of serviceable sight to the line of direct vision is compensated by the mobility of the eyeball, which turns successively in different directions; thus shifting the field of vision and examining in turn every point attainable by the eye. In reading a printed page, the eye follows the lines from left to right, seeing each letter and word in succession. At the end of a line, it returns suddenly to the next, repeating this movement from the top to the bottom of the page.

The deficiency of distinctness outside the line of direct vision depends on two causes, both of which contribute to the result, namely: 1st, inaccurate focussing of the rays; and 2d, diminished retinal sensibility.

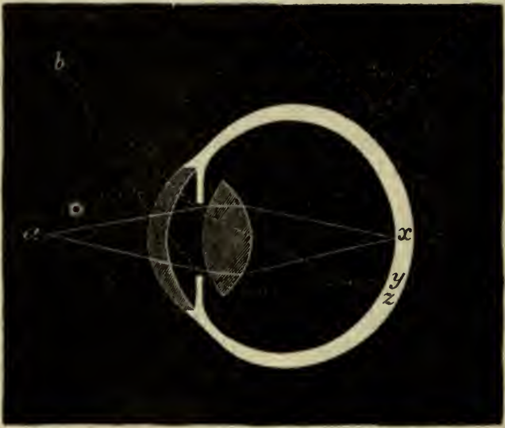
Rays of light entering the eye from the front, in the line of direct vision, are brought to a focus at the retina. But those which enter with a certain degree of obliquity suffer more rapid convergence, and are accordingly brought to a focus and again dispersed before reaching the retina. Thus rays diverging from the point *a* (Fig. 139), in the line of direct vision, are concentrated at *x*, and form a distinct image on the retina at that point. But those coming from *b*, on one side, under a similar degree of divergence, fall upon the cornea and the crystalline lens in such a way that there is more difference in their angles of incidence, and consequently more difference in the amount of their refraction. They are therefore brought together too rapidly, and are dispersed at the retina over the space *y*, *z*, forming an imperfect image. Ophthalmoscopic examination of the retina shows that, in point of fact, images formed at the fundus of the eye, in the line of direct vision, present distinct outlines; while those at a distance from this point, toward the lateral parts of the retina, are comparatively ill-defined.

Secondly, the sensibility of the retina is less acute in its lateral regions than at the fundus and the macula lutea; since according to Helmholtz, the sharpness of sight for objects at a distance from the line of direct vision diminishes more rapidly than the distinctness of their images on the retina. Objects in the visual axis are seen by *direct* vision, and are distinctly perceived; those situated within the field of view, but outside this axis, are seen by *indirect* vision, and appear more or less confused in outline.

Point of distinct vision, and Accommodation for different distances.—An optical instrument, composed of refracting lenses, cannot be made to serve at the same time for near and remote objects. If a refracting telescope or spy-glass be directed toward any part of the landscape, only the objects at a certain distance are distinctly seen; those within or beyond this distance, are obscure or imperceptible. This is because a system of lenses can bring to a focus at one point only those rays which strike its surface within a certain degree of divergence. The formation of a visible image at the desired spot depends on the refracting power of the lenses being such, that all rays diverging from the object shall be brought to a focus at the plane where its image is to be perceived. If the object be at an indefinite distance on the horizon, or if it be one of the heavenly bodies, the rays from any point of its surface reach the telescope under so slight a degree of divergence that they are nearly parallel; and, on suffering refraction, they will be brought to a focus a short distance behind the lens. But rays emanating from an object less remote, strike the lens under a higher degree of divergence. The same refractive power, therefore, brings them together less rapidly than before, and they come to a focus at a greater distance behind the lens. To provide for this, the spy-glass is furnished with a sliding tube, by which the distance of the eye-piece from the object-glass may be shifted at will. For examination of remote objects, the eye-piece is pushed forward, to bring into view the image formed a short distance behind the lens; for that of near objects it is drawn backward, to receive the image placed farther to the rear. This is the accommodation of the spy-glass for vision at different distances.

There is a similar necessity in the eye. If one eye be covered, and two vertical needles be placed in front of the other, in nearly the same linear range, but at different distances—one, for example, at eight, and the other at twenty inches from the eye—it will be found that they cannot both be seen distinctly at the same time. When we look at the one nearer the eye, so as to perceive its form distinctly, the image of the more remote one is confused; and when we see the more distant object in perfection, that which is nearer loses its sharpness of outline.

Fig. 139.



Diagrammatic Section of the Eyeball, showing difference of refraction for direct and indirect vision.—*a*, *x*. Rays from a point in the line of direct vision, focussed at the retina. *b*, *y*, *z*. Rays from a point outside the line of direct vision, brought to a focus and dispersed before reaching the retina.

The same thing may be shown by stretching in front of the eye, at the distance of seven or eight inches, a gauze veil, or other woven fabric of fine threads, with tolerably open meshes, so that objects may be visible through its tissue. The observer, in using a single eye, may fix at will either the threads of the veil, or the objects beyond it; but they alternate with each other in distinctness, like the two needles in the foregoing experiment. When the threads are sharply defined, everything else is indistinct; and when the eye is fixed on the more distant objects, so that they are sharply delineated in the field of vision, the threads of the veil become almost imperceptible, and hardly interfere with the images beyond.

It is evident, therefore, that the eye cannot perceive distinctly, at the same time, objects at different distances, but it must fix alternately the nearer and the more remote, and examine each in turn. It is also evident that, in thus shifting the sight from one object to the other, there is some change in the condition of the eye, by which it adapts itself to the distance of the object examined; and the alteration thus produced is not quite instantaneous, but requires a certain time for its completion. This process is the *accommodation of the eye for vision at different distances.*

The method by which this is effected is an important part of the physiology of sight. Its principal conditions, so far as they have been ascertained, are the following:

I. *Accommodation for different distances is accompanied by a change in distinctness of the images upon the retina.*

This is demonstrated by the observations of Helmholtz with the ophthalmoscope. When the retina is brought into view by this instrument, if the person under examination fix his attention upon a distant object, its image appears upon the retina with distinct outlines; but on changing his point of vision to a near object, the latter image becomes distinct, while the former loses its sharpness. This indicates that the result is not produced simply by mental effort, but depends on a change in the refractive condition of the eye.

II. *Accommodation for distant objects is a passive condition; that for near objects is caused by muscular activity.*

This is in some degree apparent from the accompanying sensation. The eye rests without fatigue for an indefinite time upon remote objects; but examination of those in close proximity, especially if prolonged, requires a certain effort, which, after a time, amounts to fatigue. Solutions of atropine, which, when applied to the eye, cause relaxation of the sphincter of the iris and dilatation of the pupil, suspend at the same time the power of accommodation for near objects, while that for remote objects remains perfect. Furthermore, in certain cases of paralysis of the oculomotorius nerve, not only the external muscles of the eyeball and the sphincter pupillæ are relaxed, but accommodation is also interfered with; and in these instances, according to Helmholtz, the eye remains adapted for long distances.

III. *In accommodation for near objects, the crystalline lens becomes more convex,* thus increasing its refractive power. This is the change upon which accommodation is directly dependent. It was first demonstrated by Cramer and Donders,* by the aid of "catoptric images," or images of reflection in the eye. If a candle flame be so disposed, in a room with dark walls, that its rays fall somewhat obliquely upon the cornea, and at an angle of about 30 degrees with the line of sight,

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* Donders, Accommodation and Refraction of the Eye. London, 1864, p. 10.

and if the observer place himself on the opposite side, at an equal angle with the line of sight, three reflected images of the flame will become visible, as in Fig. 140.

The first image (*a*), which is the brightest, and upright, is reflected from the cornea. The second (*b*), which is also upright, but much fainter, is from the convex anterior surface of the lens; and the third (*c*), which is tolerably distinct, but inverted, is from the posterior surface of the lens, acting as a concave mirror. If the person under observation now change his point of sight, from a distant to a near object, the eyeball remaining fixed, the second image (*b*) becomes smaller, and places itself nearer the first. This indicates that the anterior surface of the lens becomes more prominent, and approaches the cornea; but there is no change in the other two images, showing that the curvatures of the cornea and posterior surface of the lens remain unaltered.

Fig. 140.

Catoptric Images in the Eye.—*a*. Upright image of reflection, from the cornea. *b*. Upright image, from the anterior surface of the lens. *c*. Inverted image, from the posterior surface of the lens. (Helmholtz.)

Helmholtz has made these phenomena more apparent by employing, instead of a single light, two sources of illumination in the same vertical line (Fig. 141). This gives two catoptric images, one above the other, for each surface of reflection; and a change in convexity of either one would be manifested by the approach or separation of its images. In accommodation for remote objects (*A*), the images from the anterior surface of the lens are rather large and widely separated; in accommodation for near objects (*B*), they diminish in size and approach each other. The reflections from the cornea and those from the posterior surface of the lens remain at the same distance in both states of accommodation.

Fig. 141.

Change of Position in Double Catoptric Images during accommodation.—*A*. Position of the images in accommodation for distant objects. *B*. Position of the images in accommodation for near objects. *a*. Corneal image. *b*. Image from anterior surface of lens. *c*. Image from posterior surface of lens. (Helmholtz.)

The advance of the iris and pupil, from protrusion of the anterior face of the lens, in accommodation for near objects, can be observed, as remarked by Helmholtz, by looking into the eye from the side. The person under observation fixes his sight upon a distant object, and the observer places himself in such a position that the edge of the iris is just concealed by the sclerotic. If the sight be now shifted from the distant object to a nearer one in the same linear range, the pupil visibly advances toward the cornea, and the iris shows itself a little in front of its former position. If the sight be again directed to the distant object, the pupil recedes and the edge of the iris disappears behind the sclerotic.

The accommodation of the eye for near objects is therefore produced by *increased refractive power of the lens*, from the greater bulging of its anterior face. This increases the convergence of rays passing through it, and compensates for their greater divergence beforehand. In the condition of ocular repose, with the eye directed to distant objects, rays coming from any one point arrive at the cornea nearly parallel, and are so refracted as to meet in a focus at the retina. When the eye is directed to a nearer point, the lens increases its anterior convexity; and the divergent rays, being more strongly refracted, are still brought to a focus at the retina, as before. It thus becomes possible to fix alternately, in distinct vision, objects at various distances.

Mechanism of Accommodation.—The means by which the lens is rendered more convex, in vision for near objects, is not fully demonstrated. Reasons have already been given for the belief that it is accomplished, in some way, by muscular action; and the two muscles which, separately or together, undoubtedly produce this change, are the *iris* and the *ciliary muscle.*

The pupil certainly contracts in accommodation for near objects. This is easily observed on examining by daylight an eye which is alternately directed to near and remote objects. The ciliary muscle, on the other hand, cannot be inspected in this way; but its attachments and position have led many writers to consider it as the principal agent in changing the form of the lens.

It appears that the diminution in size of the pupil is not by itself an efficient cause of accommodation; since, according to Helmholtz, if the observer look through a perforated card, the orifice of which is smaller than the pupil, near objects still appear indistinct when the sight is directed to the distance, and *vice versâ*, notwithstanding the invariable dimensions of the artificial pupil employed. The contraction of the sphincter pupillæ probably serves to fix the inner border of the iris, as a point of attachment for its radiating fibres. These fibres are attached externally to the elastic tissue at the posterior wall of the canal of Schlemm (Fig. 130); and from this circle also arise the fibres of the ciliary muscle, which radiate thence to their attachment at the choroid membrane. If the circular and radiating fibres of both muscles contract together, they will form a connected system, which may exert a pressure on the borders of the lens, sufficient to cause the protrusion of its anterior face. The details of this mechanism are by no means clearly understood; and explanations, varying more or less from the above, have been proposed by observers of high authority. The direction and degree in which pressure would be exerted, by muscular fibres attached like those in the interior of the eye, are too imperfectly known to warrant a positive statement in this respect.

Limits of Accommodation for the Normal Eye.—The normal eye is so constructed that rays emanating from a single point, though coming from an indefinite distance, and therefore sensibly parallel, are brought to a focus at the retina (Fig. 142). Vision is accordingly distinct, even for the heavenly bodies, provided their light be neither too dim nor too brilliant. For objects situated nearer the eye, the convexity of the lens increases with the diminution of distance, and vision remains perfect. But there is a limit to the change in shape, of which the lens is capable; and when this limit is reached, a closer approximation of the object destroys the accuracy of its image. For ordinary normal eyes, in the early or middle periods of life, accommodation fails and vision becomes indistinct, when the object is placed at less than 15 centimetres (6 inches) from the eye.

Between these two limits, of 15 centimetres and infinity, the accommodation required is by no means in simple proportion to the distance. The accommodation necessary for objects situated respectively at 15 and 30 centimetres from the eye (6 inches and 12 inches), is much greater than for the distances of one yard and two yards. The farther the object recedes from the eye, the less difference is produced, in the divergence of the rays, by an additional distance; and consequently less change is required in the refractive condition of the eye. It is generally found that no sensible effort of accommodation is needed for objects situated beyond fifty feet from the observer; while within this limit the accommodation necessary for distinct vision increases rapidly with the diminution of distance.

An eye which is capable of distinct vision, throughout the whole range between 15 centimetres and an indefinite distance, is, in this respect, a normal eye, and is said to be *emmetropic;* that is, its powers of accommodation are within the natural limits or measurements of this function.

Presbyopic Eye.—The power of accommodation naturally diminishes with the advance of age; and observation shows that this diminution dates from the earliest period of life. Infants often examine minute objects at very short distances, in a manner which would be impracticable for the healthy adult eye; and the minimum distance of distinct vision at twenty years of age is placed by some writers at ten centimetres instead of fifteen. The power of increasing the convexity of the lens to this extent is soon lost; and, as it continues to diminish, a time arrives, usually between the ages of 40 and 50 years, when the incapacity of accommodation for near objects begins to interfere with the ordinary occupations of life. When this condition is reached, the eye is said to be *presbyopic.* Its vision is still perfect for distant objects, but it can no longer adapt itself to those in close proximity. To remedy this defect the patient employs a convex eye-glass, which gives him an increased refraction for the examination of near objects; and he is thus enabled to read or write at ordinary distances and in characters of the ordinary size.

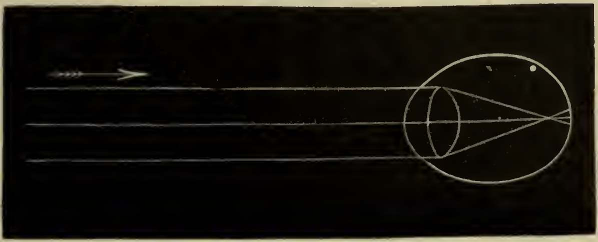
The use of a convex eye-glass does not restore the perfection of sight as it existed beforehand. In the normal eye, the degree of accommodation varies for every change of distance within fifty feet; and the organ is thus adjusted by an instantaneous and unconscious movement, for the most delicate variations of refractive power. But an eye-glass, the curvatures of which are invariable, can give perfect correction only for a single distance. A glass is, therefore, usually selected of such curvature as to serve for the most convenient distance in ordinary manipulations.

Myopic Eye.—In many instances, where the eye is otherwise normal, its antero-posterior diameter is longer than usual, thus placing the retina at a greater distance behind the lens. Consequently, although the rays are brought to a focus at the usual distance behind the cornea, this focus is situated in the vitreous body; and the rays reach the retina only after their crossing and partial dispersion (Fig. 143). This produces indistinct vision for remote objects. But for those at shorter distances, the rays enter the pupil under such a divergence, that their focus falls at the retina, and the object is distinctly seen. Such an eye is said to be *myopic*, or, in ordinary language, "near sighted," because its range of distinct vision is confined to comparatively near objects. The flexibility of the lens, and its capacity for increased convexity, may be, in the myopic eye, fully up to the normal standard, and consequently its power of accommodation may be as great as that of the normal eye. In the emmetropic condition, a certain variation in the curvature of the lens produces the requisite accommodation for all distances between 15 centimetres and infinity. In the myopic eye the same accommodating power may be exercised between the distances of 8 and 20 centimetres. The myopic eye consequently has distinct vision at

FIG. 142.

EMMETROPIC EYE, in vision at long distances. (Wundt.)

FIG. 143.



MYOPIC EYE, in vision at long distances. (Wundt.)

shorter ranges than a normal one, but gives an imperfect image for remote objects.

The remedy employed for the myopic eye is a concave eye-glass, which increases the divergence of the incident rays. This serves to carry the focus of parallel or nearly parallel rays farther backward, so that it falls upon the retina, producing distinct vision. As the accommodating power is normal in amount, this contrivance restores the perfection of sight, if the eye be otherwise well-formed; and the patient can then accommodate for all distances within the natural limits of distinct vision.

Apparent Position of Objects, and Binocular Vision.—The apparent position of an object is determined by the direction in which the luminous rays coming from it enter the eye. The perception of light necessarily marks the direction in which it has arrived, and therefore the apparent position of its source. It is difficult to understand fully the physiological cause for this appreciation of the path followed by a luminous beam; though it seems probable that it may be connected with the position of the rods and cones, which are everywhere perpendicular to the curved surface of the retina, and thus receive the impression of a ray, if at all, in the direction of their longitudinal axes. But whatever may be the optical mechanism of the process, its result is that a ray coming from below attracts attention to the inferior part of the field of vision; and one coming from above is referred to the upper part of the same field. Thus if two luminous points appear simultaneously in the field of vision, they present themselves in a certain position with regard to each other, above or below, to the right or the left, according to the direction in which their light has reached the eye.

It is evident accordingly that the lower half of the retina receives the rays coming from above, and its upper half those coming from below; while the right half of the visual field is perceived by the left half of the retina, and *vice versâ*. The image formed upon the retina is consequently an inverted and reversed image of the object. But as it is the direction of the visual ray at its impact on the retina which determines the apparent position of its source, objects will appear erect, though their images on the retina are inverted; and the eye perceives every object in the field of vision above or below, to the right or left, according to the position which it really occupies in regard to the centre of the field and the line of direct vision.

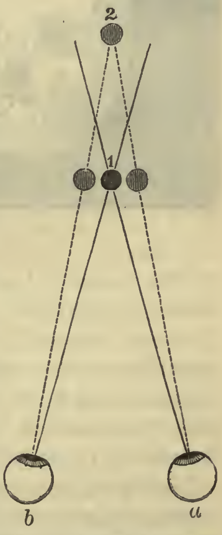
Point of Fixation, in Vision with Two Eyes.—For either eye, distinct perception is possible, as shown above (p. 538), only for objects in a single range, known as the "line of direct vision." Since the eyes are placed in their orbits at a lateral distance from each other of about six centimetres, when they are both directed at the same object, within a moderate distance, their lines of direct vision have a sensible convergence, and meet at a certain point. At this intersection of the two lines of direct vision, an object may be seen distinctly by both eyes. But at every other point it must appear indistinct to one of them; because if in the line of direct vision for the right eye it will be out of that line for the left eye, and *vice versâ*. There is, accordingly, only a certain distance, directly in front, at which an object can be distinctly seen simultaneously by both eyes; namely, that at which the two lines of direct vision coincide. This point is called the *point of fixation* for the two eyes. In fixing any object, for binocular vision, the accommodation in each eye is adjusted for the required distance; and thus the entire accuracy of both organs is concentrated upon a single point.

Since it is the position of the two eyes in their orbits which determines the point of fixation, the observer can form a tolerably accurate judgment, as to whether another person within a moderate distance be looking at him, or at a different object in the same direction. For greater distances the estimate fails, because the obliquity of the eyes, in looking at remote objects, is so small that its variation is no longer appreciable.

Single Vision with both Eyes.—It is evident from the preceding that there can be only one point in the line of direct vision for both eyes at the same time. When an object occupies this situation, namely, the point of fixation, it is distinctly perceived by each eye in the centre of the field of vision; thus its two visual images exactly cover each other and so form but one. Consequently, the object appears single, though seen by both eyes. But if placed either within or beyond the point of fixation, it will appear indistinct and at the same time double. If the observer hold a slender rod in the vertical position at a distance of one or two feet before the face, and in the same range with any small object, such as a door-knob, on the opposite side of the room, it will be found that when both eyes are directed at the rod, it is seen single and distinctly, but the door-knob appears double, one of its images falling on each side. If the eyes be now directed at the door-knob, that in turn becomes distinct and single, while the figure of the rod is double, one indistinct image appearing on each side, as before.

These phenomena depend on the different directions of the two lines of vision. When the nearer object (Fig. 144, $_1$) occupies the point of fixation, the farther object ($_2$) will also be seen, because it is still included in the visual field; though it will be seen indistinctly, because the accommodation of the eye is not adjusted to its distance, and because it is not in the direct line of sight. But for the right eye (*a*) it will be placed to the right of this line, and for the left eye (*b*) to the left of it. Its two images do not correspond with each other in situation, and it accordingly appears double.

FIG. 144.



SINGLE AND DOUBLE VISION, at different distances.—*a.* Right eye. *b.* Left eye. 1. Object at the point of fixation, seen single. 2. Object beyond the point of fixation, seen double.

When the eyes, on the other hand, are directed to the more distant object, the nearer one is no longer at the point of fixation. For the right eye, its image will appear to the left of the line of sight, and for the left eye to the right of this line. It therefore becomes double and indistinct.

Thus, in ordinary binocular vision every object but one appears double and indistinct. This circumstance is so little noticed that it never causes confusion of sight, and even requires a special experiment to demonstrate its existence. The reason for its passing unobserved is twofold. First, the attention is naturally concentrated upon the object at the point of fixation. When this point is shifted, each new object upon which it falls appears single; and thus the idea of a double image, even if indistinctly suggested at any time, is at once dispelled by the movement of the eyes in that direction. Secondly, an object placed toward either side will form a double image, since its apparent position is different for the two eyes. But the obliquity of its rays, and consequently the indistinctness of its image, will be greater for the right eye than for the left, or *vice versâ;* and the notice of the observer, if drawn to it at all, is occupied with the more distinct of the two images, to the exclusion of the other. The fact becomes palpable only in such an experiment as the above, where the bodies examined are in the same linear range, so that the double images produced are equal in intensity, and sufficiently contrasted with surrounding objects to attract attention.

FIG. 145.

AS SEEN BY THE LEFT EYE.

FIG. 146.

AS SEEN BY THE RIGHT EYE.

Double vision may be produced at any time by pressure at the outer angle of one eye, so as to alter its position in the orbit, the other eye remaining fixed. But in this case the whole field of vision is displaced, and all objects are doubled indiscriminately. This form of double vision is produced, in vertigo or intoxication, by irregular action of the muscles of the eyeball.

Appreciation of Solidity and Projection.—When both eyes are directed at a single object, its distance may be estimated with some accuracy by the convergence of the visual axes required for its fixation. Another impression is also produced by binocular vision, when an object, of appreciable volume and thickness, is viewed within a moderate distance. Owing to the lateral separation of the two eyes, and the convergence of their visual axes, they do not receive precisely the same image. Both eyes will see the front of the object in nearly the same manner; but in addition the right eye will see a little of its right side, and the left eye a little of its left side. This is illustrated in Figs. 145 and 146, representing an object as seen by the two eyes, at a distance of eighteen inches or two feet; rather more of the details on one side being visible to the left eye, and rather more of those on the other side to the right eye. As the central part of its mass is in the point of fixation, at the junction of the visual axes, the object appears single. But the images which it presents to the two eyes are not precisely identical; and the combination of these different images into one gives the impression of *solidity* and *projection.*

This effect is complete only when the object is within a moderately short distance. For those which are remote, the convergence of the visual axes, and the consequent difference in configuration of the images, become inappreciable, and the impression of solidity disappears. At a distance of some miles even a large object, like a mountain, loses its projection, and appears like a flattened mass against the horizon. The pictorial representation of distant views is therefore often very effective, the idea of remoteness in different parts of the landscape being conveyed by appropriate intersections of outline and by variations in tone, color, and distinctness, like those due to the interposition of the atmosphere. But a picture which aims to represent the solidity of near objects can never deceive us in this respect, however elaborate its details; since its surface presents the same image to both eyes, and it is consequently evident that the objects delineated have no real projection. But the appearance of solidity may be successfully imitated by representing an object in two different positions. This is the principle of the *stereoscope.* Two photographic pictures of the same object are taken from different points of view, one of them representing it as it would be seen by the right eye, and the other as it would be seen by the left. With these pictures so placed in the stereoscope that each eye has presented to it the appropriate view, the two images are combined in the act of vision, producing the apparent effect of projection and solidity.

General Laws of Visual Perception.—Beside the formation and combination of optical images, there are certain phenomena connected with visual perceptions in general which are of interest in the physiology of sight. Some of these phenomena require special modes of investigation, while others are made evident by comparatively simple means, and are often important in their hygienic relations.

Luminous impressions upon the eye continue for a short time after *cessation of the light.*—The persistence of these impressions is not usually noticeable, because they are immediately followed by others on the same part of the retina, and are thus practically obliterated. But, if the momentary impression be not at once followed by a different one, or if sufficiently vivid to be perceived, notwithstanding the presence of others, it may be made evident to observation. If a bright point, like the heated end of a wire, be carried round in a circle in a dark room with moderate rapidity, the eye follows it throughout. But if the rapidity of its movement be increased, it appears drawn out more or less into a curved line; and, when moving with very high velocity, it becomes transformed into a continuous circle of light, since its impression upon the retina, when at one part of the circle, lasts until it has completed its revolution and returned to the same point. The sparks thrown off in rapid succession from a knife-grinder's wheel produce the effect of an unbroken stream of fire. A circular saw with large teeth, revolving under high speed, presents apparently a smooth edge, formed by the moving points of the teeth; and the spokes of a rapidly-turning wheel become confused upon the retina with the intervening spaces, and assume the appearance of a glimmering disk.

The duration of visual impressions cannot be expressed by any single term which would be correct for all cases. A brilliant light leaves, on the whole, a longer impression than a feeble one; but, on the other hand, its relative intensity to surrounding objects diminishes more rapidly, and it consequently requires, if in motion, a higher velocity to produce the appearance of a uniform bright line. The time during which luminous impressions remain, without appreciable diminution of their intensity, is usually tested by means of revolving disks, variegated in equal sectors of black and white. The rate of revolution being known, as well as the width of the sectors, when the revolving surface presents a uniform gray tint, the time during which the visual impression remains undiminished is readily calculated. The result of such experiments gives the duration of undiminished impressions, for revolving disks under moderate illumination, as one-twenty-fourth of a second; and, for the oscillation of a very luminous point following the vibrations of a tuning-fork, one-thirtieth of a second.

The persistence and apparent continuity of successive visual images are illustrated by the *Thaumatrope* and other similar contrivances, in which a number of pictures, representing the same object in different positions, are made to pass in quick succession before the eye. The intervals between them are too short to be observed, and the figure appears as if in motion.

Duration of a Luminous Impulse necessary for its Perception.—This point has been investigated by Rood[*] by means of the electric spark from an induction coil connected with a Leyden jar. The dura-

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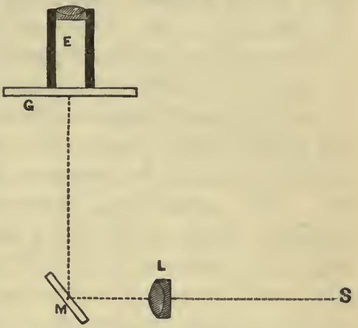
[*] American Journal of Science and Arts. New Haven, September, 1871.

tion of the spark obtained on breaking the primary current was measured by the aid of an apparatus arranged as in Fig. 147.

The light emanating from the spark, S, was received by an achromatic lens, L. It then fell upon a plane mirror revolving with a uniform velocity of 340 per second, and, after reflection, was brought to a focus upon a glass plate, G, where it could be examined by the eye-piece, E, magnifying ten diameters. From the known rate of revolution of the mirror, and its distance from the plate G, the rapidity of motion of the reflected beam upon the plate was determined. If the spark lasted long enough for its reflected image to move over an appreciable distance, it would appear to be drawn out in a linear form, owing to the persistence of its visual impression. But with the mirror revolving at this speed no such alteration was perceptible, the reflected spark appearing as if stationary; showing that the duration of the light could not be greater than .000002 ($\frac{1}{500000}$) of a second.

FIG. 147.



APPARATUS for measuring the duration of an electric spark.—S. Position of the spark. L. Achromatic lens. M. Revolving mirror. G. Glass plate for receiving the image of the spark. E. Telescope eye-piece.

In subsequent experiments, there was interposed between the spark and the mirror a glass plate, ruled with alternate transparent and opaque lines, $\frac{1}{24}$ of a millimetre in width. Its image, when illuminated by the spark, would appear upon the plate, G, as a series of black and white lines. With the mirror in motion, if the illumination lasted long enough for the image to be shifted a distance equal to the combined width of a black and white line, these lines would become undistinguishable from each other as in the revolving disk with black and white sectors. Thus the continuance of the visible lines, under a given rate of motion, proved that the duration of the electric spark was less than a certain calculable period. The result showed that the shortest measurable spark lasted but little over .00000004 ($\frac{1}{25000000}$) of a second.

With a spark of this duration, motionless objects were distinctly visible. The letters on a printed page could be recognized, and even the polarization of light was plainly observable. It was accordingly sufficient to produce a complete retinal impression.

These experiments do not indicate the time required for nervous action in the perception of light. They only show that a luminous impulse having the above duration is sufficient to excite the sensibility of the retina. But the time required for perceiving the sensation is very much longer. From the results given in a preceding chapter (page 371) it appears that the passage of a visual impression through the optic nerve would require at least $\frac{1}{1000}$ of a second, and its perception in the brain considerably more. It follows from this that, at the instant when the electric spark is seen, it has, in fact, already come to an end; the interval which elapses before it is perceived by the observer being very much greater than its actual duration.

This accounts for a peculiar effect, often observed under the use of the electric spark, namely: that bodies in rapid motion, when illuminated by an instantaneous discharge, appear as if at rest. A disk with black and white sectors, in revolution under continuous light, appears of a uniform gray. But if such a disk, revolving in a dark room, be illuminated by the electric spark, it becomes visible for an instant, with its sectors as distinct from each other as if they were at rest. A jet of water, flowing from a narrow orifice, is transparent in its upper part, but turbid lower down; and by instantaneous illumination the turbid portion is seen to be composed of separate drops, which appear motionless. The passage of a cannon-ball or a bullet by daylight is imperceptible; because it does not remain long enough at any one point to efface the persistent impression of objects behind it. But if such a missile should happen to be passing in front of the observer in the night during a thunder-storm, at the moment of a flash, it would be equally visible with other objects, and would appear as if suspended motionless in the air.

The momentary closure of the eyes in winking, for the same reason, is unnoticed, and causes no interference with sight; since the visual impression of external objects continues unimpaired during the interval occupied by the movement of the lids.

The sensibility of the retina is diminished by continued impressions.—This diminution seems to take place from the very commencement of a visual impression, so that it may be perceptible within a few seconds. When the image of the retinal blood-vessels is made apparent by changing the position of their shadows (page 530) their figures are visible for an instant with extreme sharpness. But they at once begin to fade and soon become imperceptible. The portions of the retina under full illumination have their sensibility so rapidly diminished, that the shadow, if motionless, is no longer visible by contrast. Those in shadow, on the other hand, become more sensitive by repose; and when the shifting of the light brings them again into illumination, they are already more susceptible to its influence.

If one eye be covered by a dark glass, and the other used alone for reading or writing, at the end of an hour the difference in retinal sensibility of the two will be very apparent. A faintly luminous object in a dark room may be almost imperceptible to the eye which has been in use, while appearing to the other quite brilliant. But this condition is transitory; and by covering the eye previously in use, and reading or writing with the other, the fatigued organ recovers its sensibility, and that which was before the most sensitive becomes less so.

The diminution and recovery of retinal sensibility, under excitement and repose, is connected with the phenomena of *negative images.*

If the eye be fixed for a short time upon a white spot in a black ground, and then suddenly directed toward a blank wall of white or light gray color, a dark spot will appear upon it, of the same size and figure with the white one previously observed. This is the "negative image" of the retinal impression. That part of the retina which was first impressed by the rays from the white spot becomes less sensitive; and another white surface, looked at immediately afterward, appears dark. On the other hand, those parts which were exposed only to the dark ground, that is, to the comparative absence of light, are more sensitive than before; and the surface of the white wall, outside the central spot, consequently appears brighter. If a piece of dark furniture against a white or gray wall be looked at steadily for a short time, on shifting the eyes to a different part of the wall, the figure of the chair or table will appear, with all its details of outline, expressed in a lighter tint than that of the surrounding parts.

Negative images may be produced in a still more simple manner. Let a black ruler, about one inch wide, be laid upon a sheet of white paper, and looked at steadily for thirty or forty seconds. If the ruler be now suddenly removed, the eye remaining fixed, its image will appear as a bright band upon the paper, gradually fading as the retinal sensibility becomes equalized.

The sensibility of the retina may be separately increased or diminished for different colors. If a black ruler be laid upon a blue cloth, on taking it away a band appears in its place of a more intense blue than the rest; and if placed upon a red cloth, its negative image is of a remarkably pure red, the remainder appearing of a dull brown. But parts of the retina which have been fatigued by the continued impression of one color are more sensitive to rays of the complementary hue; since the latter have been for a certain time excluded. A strip of red paper, placed on a white ground and suddenly removed, leaves an image which is bluish-green; and a green one leaves an image with a tinge of red. The light from the white ground really contains all the colors; but an eye which has become less sensitive to green rays will receive an impression in which the red predominates, and *vice versâ.*

Owing to the variable sensibility of the retina, according to exposure, an object, under some conditions, is most easily perceived by indirect vision. It often happens that a small and feeble star may be momentarily perceived by looking, not directly at it, but at some point in its immediate neighborhood. The star is not seen distinctly under these circumstances, because it is out of the line of direct vision. But its light falls upon a part of the retina near the fovea centralis, where the sensibility is more acute than usual, owing to its previous exposure only to the dark sky; while the fovea itself, which has been receiving in succession the images of various stars, is comparatively deficient in sensibility. When the visual axis is turned directly upon the faint star, in order to get a distinct view, its light disappears. It can only be seen as an evanescent object by indirect vision.

Sense of Hearing.

By the sense of hearing we receive the impressions of sound, and appreciate their intensity, their higher or lower notes, and their quality, that is, the different character of sounds of similar pitch and intensity, produced by different means, as by reeds, strings, or wind instruments, or the concussion of solid or liquid bodies. Our idea of *time*, or the succession of events, seems also especially connected with auditory sensations. Impressions received in this way depend on the vibrations excited in the atmosphere by sonorous bodies, which are themselves already in vibration. These undulations, when communicated to the auditory apparatus, produce, through it, the sensation of sound.

Organ of Hearing.—The organ of hearing consists of, first, the *external ear*, a trumpet-shaped expansion, which collects the sonorous impulses coming from various quarters, and conducts them into its tubular continuation, the external auditory meatus; secondly, a membranous sheet or drum-head, the *membrana tympani*, stretched across the auditory meatus, by which the vibrations are received and transmitted, through the chain of bones in the tympanum, to the *labyrinth*, or internal ear; a cavity in the petrous portion of the temporal bone, containing various membranous sacs and canals, upon which are distributed the filaments of the auditory nerve.

Thus the terminal expansions of the auditory nerve, deeply concealed in their bony cavities, and sustained by the surrounding fluids, while protected from all other mechanical impressions, are so placed as to receive the impulse of sound.

External Ear.—The external ear is a cartilaginous framework, covered with integument, and more or less movable by various muscles, which turn it in various directions. In man, these muscles are nearly inactive; though in exceptional cases they can produce a partial sliding or rotatory movement of the ear. In most quadrupeds, on the other hand, the movements are vigorous and extensive, and greatly aid in the sense of hearing, by enabling the organ to catch distinctly the sonorous vibrations, from whatever quarter they come. They also serve to indicate the direction of a sound, since the animal ascertains, by placing the ear in different positions, the region from which it is received with greatest distinctness.

Membrana Tympani and Chain of Bones.—The membrana tympani is a circular fibrous sheet not more than 0.05 millimetre in thickness, but quite strong, consisting of circular and radiating tendinous fibres, with a trace of intermingled elastic tissue. Its outer and inner surfaces respectively are covered by thin continuations of the integument of the external auditory meatus, and of the lining membrane of the tympanic cavity; and the three layers combined form a membrane about 0.10 millimetre in thickness.

In its natural position the membrane is drawn inward, by its attachment to the malleus, in such a way as to present a funnel-shaped depression, the deepest point of which corresponds to the end of the handle of the malleus. According to Helmholtz,* the sides of this depression are convex, somewhat like the inner surface of the blossom of a morning-glory. It is only along a line corresponding to the handle of the malleus, that the meridian of the funnel is a nearly straight line; elsewhere the radial fibres of the membrane are curved, with their convexities toward the external auditory meatus.

As the only attachment of the membrana tympani, except at its border, is to the handle of the malleus, any movement of this bone inward will draw the membrane in the same direction, deepen its central depression, and put its fibres upon the stretch. On the other hand, if the membrane be forced outward, it will draw the handle of the malleus with it; and, finally, if the elastic and muscular attachments generally be in equilibrium, any movement of the membrane will be followed by a corresponding change of position in the malleus.

This is the physiological action of the membrana tympani. From its thinness and tension, and from its position at the bottom of the external auditory meatus, it enters into vibration, under the impulse of sounds from the exterior, and communicates its movement to the handle of the malleus at its inner surface.

The chain of bones consists of three ossicles, articulated with each other by their extremities, and forming a zigzag line of jointed levers across the cavity of the tympanum. They are known respectively, from their configuration, as the "malleus," "incus," and "stapes," or the hammer, the anvil, and the stirrup. The malleus is about nine millimetres in length, of which a little more than one-third is occupied by the rounded head and the neck, and a little less than two-thirds by the comparatively straight and tapering handle. Its very slender lateral process projects in a nearly horizontal direction from behind forward in the natural position of the bone. The handle is the only part of the malleus adherent to the membrana tympani, the neck corresponding to the upper border of this membrane, while the head projects above it, lying comparatively free in the tympanic cavity. It is maintained in position by thin ligamentous bands from the bony wall of the cavity inserted into its head and neck, and by the tendon of the internal muscle of the malleus or "tensor tympani." The action of this muscle is to draw the handle of the malleus inward, tightening the membrana tympani, and rotating the head of the bone slightly out-

Fig. 148.

Ossicles of the human ear.—1. Malleus. 2. Incus. 3. Stapes. (Rüdinger.)

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* Mechanism of the Ossicles of the Ear. Buck's Translation. New York, 1873, p. 20.

ward. When in movement, the malleus oscillates about a nearly horizontal axis situated at the junction of its handle and neck.

The head of the malleus is articulated with the incus by a capsular joint with double-inclined surfaces. As Helmholtz has shown, these surfaces have such an inclination, that when the handle of the malleus is drawn inward, they lock together, and the incus follows the movement of the malleus; but when the latter bone is drawn outward, they may glide upon each other, without necessarily moving the incus.

The third bone of the middle ear, the stapes, has a close resemblance in form to its namesake, a metallic stirrup. It is articulated by its angular extremity to the end of the long arm of the incus in a nearly horizontal position. Its oval base corresponds in form, and nearly in size, with the fenestra ovalis of the bony labyrinth, in which it is inserted; being adherent by its surface and its edges to the internal periosteum of the labyrinth.

Fig. 149.

Right Temporal Bone of the new-born infant, seen from its inner side; showing the membrana tympani and chain of bones in their natural position. (Rüdinger.)

The stapes, accordingly, forms a kind of movable lid or piston-head occupying the fenestra ovalis, and capable of transmitting to the fluid of the labyrinth the impulses received from the membrana tympani: The extent of inward and outward movement of the base of the stapes has been determined by Helmholtz in the following manner: The cavity of the tympanum and that of the vestibule having been opened from above, the point of a fine sewing-needle was inserted into the fibrous covering of the base of the stapes on the side of the vestibule, and the needle allowed to rest, near its insertion, upon an adjacent edge of bone. It thus formed a kind of index-lever, which would indicate by its movement very slight displacements of the stapes. The stapes was then pressed inward and outward, as freely as its attachments would allow, either by direct pressure or by condensing and rarefying the air in the external auditory meatus; the force, in the latter case, being transmitted through the membrana tympani and chain of bones. The movements were also estimated by opening the superior semicircular canal of the labyrinth, and inserting into it a slender glass tube of known calibre, a portion of which, as well as the vestibule, was filled with water; any inward pressure being indicated by a corresponding rise of the water-level in the tube. The movement of the stapes, in these experiments, varied from .025 to .072 millimetre.

The change of position of the stapes in the fenestra ovalis, from impulses received through the chain of bones, is not a simple movement of advance and recession, but a rocking motion, in which its upper border is tilted back and forward. This action of the stapes depends on the varying compactness of its fibrous attachments, which allow more freedom of movement above than below.

The position of the stapes is also regulated by the action of the *stapedius* muscle. This muscle, the smallest in the body, arises from a bony canal behind the tympanum; its slender tendon passing almost directly forward to be inserted into the neck of the stapes, near its articulation with the incus. Its contraction, therefore, draws the angle of the stapes backward, and its anterior extremity outward from the fenestra ovalis.

Physiological Action of the Bones and Muscles of the Middle Ear.—The cavity of the tympanum is an irregularly shaped space, across which the vibrations received by the membrana tympani are transmitted by the chain of bones. In their natural position and with their tendinous connections undisturbed, these bones are in such close connection with each other that they vibrate as a single body.

The action of the internal muscle of the malleus, or *tensor tympani*, is, no doubt, as its name indicates, to increase the tension of the membrana tympani. It has long been known that, after opening the cavity of the tympanum and the canal in which this muscle is lodged, by traction upon its tendon the membrana tympani is rendered more tense; and, according to Helmholtz, all the ligaments holding the ossicles in place are at the same time put upon the stretch.

The effect produced upon hearing by increased tension of the membrana tympani has been variously interpreted. Savart,* who first studied systematically the vibration of stretched membranes induced by the proximity of sounding bodies, estimated its extent from the agitation of fine sand sprinkled on the membranes; and found it less pronounced, other things being equal, when the tension of the membrane was increased. He applied the same method to the membrana tympani of man and animals, and found that sand, sprinkled on its surface, could be thrown into agitation by holding near it a sounding body, and that these phenomena were less easy of production when the membrane was rendered more tense by traction on the tensor tympani. He concluded that during life the ear is more susceptible to sounds of a given intensity when the membrana tympani is relaxed than when it is on the stretch; and that the tensor tympani, accordingly, exerts a protective action by lessening the apparent intensity of loud sounds.

But this observer was not aware of an important fact established by subsequent investigations, namely, that stretched membranes, like cords, cannot respond indiscriminately to sounds of every tone, *but*

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* Journal de Physiologie. Paris, 1825, tome iv., p. 205.

*only to a certain number of tones, separated by definite intervals;** and that they will respond to a different set only after their tension has been increased or diminished. In order, therefore, that a membrane may be easily thrown into induced vibration, its tension must correspond in a certain ratio with the tone of the sounding body.

These considerations have induced a different view of the tensor tympani as modifying the sensations of sound. With the membrane in a state of moderate tension, a certain number of tones only are distinctly appreciated, the remainder being either inaudible or indistinct. This is the state in which sounds are generally perceived, without exact appreciation of their relative pitch. But when the ear follows a succession of tones, or when it listens for a particular note, the tension of the membrane is so increased or diminished as to transmit the vibration with the greatest distinctness. With regard to modifications in the apparent *intensity* of sound, it is probable that Savart's explanation holds good; and that a diminished tension of the membrane enables the ear to catch more readily sounds which are faint or distant. This partial relaxation is accomplished by the stapedius muscle, which is animated by a filament of the facial nerve, and is therefore more directly under the control of the will; while the tensor tympani is supplied from the otic ganglion of the sympathetic, and is involuntary in its action.

The cavity of the tympanum communicates with the pharynx by the *Eustachian tube.* The existence of this canal secures equality of atmospheric pressure on both sides of the membrana tympani, a condition essential to its free vibration under sonorous impulses. The external barometric pressure varies from time to time; and if the middle ear were a closed cavity, this variation would of itself change the tension of the membrana tympani and interfere with its function. Although the walls of the Eustachian tube are habitually in contact with each other, they readily yield to atmospheric pressure in either direction, and thus reëstablish the equilibrium between the outer air and the cavity of the tympanum.

Labyrinth.—The internal ear, or labyrinth, so called from the complicated extension of its cavities, is situated in the petrous portion of the temporal bone. It may be divided into: 1. The *vestibule and semicircular canals*, which constitute its most essential parts and are present in all vertebrate animals; and 2. The *cochlea*, which, in man and the mammalia, is a more highly developed portion, but which is absent in the fishes and naked reptiles, and only partially developed in scaly reptiles and in birds.

The *vestibule* (Fig. 150, $_1$) is so called because its cavity is that into which the fenestra ovalis immediately opens, and which leads to the semicircular canals and cochlea. It has an ovoid form, and presents, on the side toward the tympanum, two openings, namely: 1. The

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* Daguin, Traité élémentaire de Physique. Paris, 1867, tome i., p. 596.

fenestra ovalis (5), corresponding in form to the base of the stapes, which nearly fills it, and which is adherent to the internal periosteum of the labyrinth; and 2. The fenestra rotunda (6) of smaller size and closed by a fibrous membrane. The posterior portion of the vestibule gives origin to the three semicircular canals, namely: 1. The superior vertical canal (2) with its plane lying across the longitudinal axis of the petrous bone. 2. The inferior vertical canal (3) the plane of which is parallel with the median surface of the petrous bone; and 3. The horizontal canal (4) lying across the axis of the petrous bone, in a horizontal plane. Each semicircular canal opens into the vestibule by two orifices, one at each end; except that the two vertical canals unite at one extremity into an orifice common to both. Each canal is enlarged at one extremity, where it joins the vestibule, into a rounded dilatation.

Fig. 150.

Bony Labyrinth of the Human Ear, twice the natural size.—1. Vestibule. 2. Superior vertical semicircular canal. 3. Inferior vertical semicircular canal. 4. Horizontal semicircular canal. 5. Fenestra ovalis. 6. Fenestra rotunda. 7. Cochlea.

This part of the bony labyrinth contains a colorless fluid—the perilymph, and, in addition, a membranous sac, also filled with fluid, which, by its prolongations, repeats the form of the vestibule and semicircular canals. This sac, with its extension in the cochlea, constitutes the *membranous labyrinth.* It forms the most important part of the internal ear, since in its walls the filaments of the auditory nerve have their terminal distribution.

In the vestibule the membranous sac is divided into two parts by a transverse partition. One of these, the smaller of the two, is the *sacculus,* a spherical vesicle, a little over 1.5 millimetre in diameter, occupying the anterior and inferior portion of the vestibule, and communicating by a narrow canal with the ductus cochlearis of the cochlea. The other, or larger sac, is the *utricle,* of ellipsoid form, measuring 3.5 millimetres in its long diameter. The utricle and the membranous semicircular canals communicate with each other in the same way as the bony cavities in which they are lodged; and each membranous canal presents, at one extremity, a rounded dilatation, known as the "ampulla."

The membranous sacs and canals are considerably smaller than the osseous cavities which contain them, and occupy nearly everywhere an eccentric position, being, at certain points, adherent to the internal periosteum, while at others they are surrounded by the perilymph. The sacculus and utricle together occupy about two-thirds of the cavity of the vestibule; and, according to Rüdinger, are so placed that neither touches the base of the stapes at the fenestra ovalis, from which they are separated by an appreciable layer of fluid. Thus sonorous impulses reach the membranous labyrinth, not directly from the stapes, but through the intermediate vibration of the perilymph.

The main point of interest in regard to the membranous labyrinth relates to the *distribution and termination of the auditory nerve.*

The auditory nerve sends to the vestibule two branches; one distributed to the sacculus, the other to the utricle and ampullæ. The mode of termination of the nerve fibres in both divisions is essentially the same. They are not distributed generally over the membrane, but terminate in well-defined spots, characterized by a thickening of the membranous wall, and by a peculiar form of epithelium provided with stiff, pointed cilia—the so-called *auditory hairs.*

In the sacculus and in the utricle, the terminal nerve spot, or "macula auditiva," is an oval plate, 3 millimetres by 1.5 in the sacculus, and 3 millimetres by 2 in the utricle. In the ampullæ, it forms a transverse fold of the membranous wall, projecting inward like the valvulæ conniventes of the small intestine, but occupying only about one-third of their circumference. Elsewhere, the sacs are lined, according to Kölliker, by a single layer of pavement epithelium cells. But at the spots in question the epithelium is twice or three times as thick as in the remaining portions, and consists of elongated cylindrical and fusiform cells. It also presents, standing upright upon its surface, the cilia, or auditory hairs, which in man are about 25 mmm. in length. The terminal fibres of the auditory nerve, which pass toward these thickened spots, may be traced, according to all recent observers, into the epithelial layer; and certain appearances give rise to the supposition that the axis-cylinder of each fibre is prolonged through a fusiform epithelium cell, and projects, in the form of an auditory hair, from its free extremity. This is inferred mainly from the similarity in appearance between the axis-cylinder of the nerve fibres and the slender downward prolongation of the fusiform cells; and from the fact that both structures are stained blackish or brown by osmic acid (Rüdinger). However this may be, there is no doubt that the projecting cilia, either mechanically or by nervous sensibility, receive and transmit the sonorous vibrations of the surrounding fluid.

A remarkable feature connected with the auditory spots of the sacculus and utricle is the so-called *otoconia*, or ear sand. This consists of calcareous grains, embedded in a gelatinous material, and forming a white, chalky-looking layer immediately over the auditory spot. The grains are rounded, elongated, or prismatic and crystalline in form; the largest measuring, according to Kölliker, about 10 mmm. in length. Their exact office is unknown, but it is evident, from their constant existence in this situation in different animals, that they have some important relation to the sense of hearing. In man, mammalians, and birds they are pulverulent. In reptiles and fish they are sometimes of friable concretions, sometimes rounded masses, hard and dense as porcelain. According to Wagner, they are completely absent only in the cyclostomi, or fishes of the lowest order, including the lamprey and hag.

Physiological Action of the Membranous Labyrinth.—The sacculus and utricle are membranous formations suspended in the fluid of the vestibule and supplied by fibres of the auditory nerve. They are the essential parts, in the auditory apparatus, for the reception of sonorous impressions. The vibrations of the atmosphere, communicated to the membrana tympani, are thence transmitted through the malleus, incus, and stapes. From the base of the stapes they pass to the perilymph of the vestibular cavity; thence, through the wall of the membranous sac, to the endolymph or fluid in its interior; and the vibration of this internal fluid acts upon the nervous terminations at the auditory spot. It is thus, through a series of intermediate vibrations, that sounds coming from without finally produce their impression on the internal ear.

Office of the Semicircular Canals.—These singular appendages have attracted special attention, owing to the constancy of their occurrence and the peculiarity of their position. The principal features of their anatomical history are the following:

1. They are always present, as portions of the internal ear, in mammalians, birds, and reptiles, and nearly always in fish; being entirely absent only in amphioxus, where there is no organ of hearing whatever.

2. They are always three in number. The only exception to this rule is found among fishes, in the lamprey and the hag; where the entire structural development is very incomplete.* In the lamprey there are two, and in the hag only one, the cavity of which is confounded with that of the utricle, forming a ring-like membranous canal.

3. The canals stand in three different planes, perpendicular to each other. One is vertical and longitudinal, in relation to the petrous bone; another vertical and transverse; and the third transverse and horizontal. They represent accordingly, by their position, the three dimensions of space; and from this circumstance it has been surmised that they serve to indicate the direction from which sounds are perceived. But subsequent researches have yielded nothing to corroborate this view; and it is evident, furthermore, that, from whatever quarter sounds may originally come, they must reach the internal ear, through the membrana tympani and chain of bones, by the same course.

Lastly, an essential point in the structure of the semicircular canals is that they are destitute of nerve fibres, and consequently wanting in sensibility. The only nervous distribution connected with them is that to the ampullæ at their extremities, but no fibres extend to the canals themselves. Their function must therefore in all probability be of a mechanical or physical nature.

In experimenting upon the internal ear in animals, it has been remarked that division or injury of the semicircular canals is followed

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* Owen, Anatomy of the Vertebrates. London, 1868, vol. iii., p. 222. Wagner, Comparative Anatomy of the Vertebrate Animals, Tulk's translation. New York, 1845, p. 227.

by a singular affection of the posture and voluntary movements, indicating disturbance of equilibrium. These phenomena were first made known by Flourens in 1825,* and have been witnessed by many subsequent observers. They are not explained by all in the same way, but there is little discrepancy in regard to their character and details. The exposure of the semicircular canals during life is impracticable, as a rule, in the mammalia, owing to the density of the petrous bone; but it can be done without much difficulty in birds, where they are surrounded by spongy osseous tissue. The pigeon has been most frequently used for this purpose.

The most striking and constant effect from injury of the semicircular canals consists of abnormal oscillatory movements of the head, with imperfect balancing of the body. These phenomena vary according to the canal which has been divided. If it be a vertical canal, the oscillation of the head is upward and downward; if it be a horizontal one, the oscillations are from left to right, and *vice versâ*. If the corresponding canal on both sides be divided, the abnormal movements are more rapid and continuous than if the injury be inflicted on one alone. The animal is still capable of preserving his equilibrium when at rest; but any attempt at movement brings on a disordered action, which makes walking, running, or flying difficult or impossible. The most simple interpretation of these results is that the animal can no longer appreciate the position of the head, and that the sense of equilibrium is consequently impaired for the body and limbs.

The manner in which the semicircular canals may contribute to the sense of equilibrium is as follows: If a goblet, filled with water, be turned round its vertical axis, it will be seen that the water does not readily turn with it; and any small objects suspended in it, or floating upon its surface, will remain in nearly the same position, while the goblet revolves through an entire circle. The adhesion of the fluid to the glass surfaces is not sufficient to communicate to it at once the motion of the vessel. Consequently the water lags behind the glass; and if any projecting object were cemented to the inside of the goblet, so as to turn with it, it would be subjected to a backward pressure, whenever the goblet was put in rotation.

Somewhat similar conditions are present in the semicircular canals. Whenever the head is rotated from side to side in a horizontal plane, a momentary increase of pressure must take place in the fluid of the horizontal semicircular canal (Fig. 150, $_4$), either toward or from the ampulla at one end; and this increase or diminution of pressure may be perceptible by the nervous expansions there situated. If the head be moved upward or downward, a corresponding change of pressure will take place in the inferior vertical canal (Fig. 150, $_3$); and if it be inclined laterally, toward the right or left, the superior vertical canal

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* Recherches Expérimentales sur les Propriétés et les Fonctions du Système Nerveux, 2me édition. Paris, 1842, pp. 452, 454.

(Fig. 150, $_2$), will experience a similar variation. Thus, although the membranous semicircular canals be not themselves sensitive to pressure, they may serve as channels for conducting an impulse to the sensitive organs in their ampullæ. The configuration of the nervous expansions in the ampullæ seems especially adapted for this purpose, since they are arranged in the form of transverse crescentic folds. In the sacculus and utricle, on the other hand, they are simply flattened prominences on the surface of the membrane.

If it be asked, why an apparatus for appreciating equilibrium should be associated with the organ of hearing, it may be remarked that in the auditory labyrinth alone there are sensitive nerve fibres distributed to an epithelium provided with hair cells, and surrounded by a watery fluid; conditions which are especially suitable for the perception of variations in pressure, and consequently for that of changes in position.

Cochlea.—The cochlea, so named from its resemblance to a snail-shell, is a spiral bony canal making two or three turns about a central axis, with its apex directed forward, downward, and outward. It is divided longitudinally by a thin, bony partition, the *spiral lamina,* which winds round its axis, following the spiral turns, but presenting externally a free border.

FIG. 151.

BONY COCHLEA OF THE HUMAN EAR, right side; opened from its anterior face. (Cruveilhier.)

From this border a fibrous membrane, the *membrana basilaris,* extends outward to the external wall of the cavity; thus forming two parallel passages, one above the other. The upper passage, which communicates at its base with the vestibule, is the *scala vestibuli.* The lower reaches to the fenestra rotunda, where the membrane, stretched across this opening, separates its cavity from that of the tympanum; it is accordingly known as the *scala tympani.* At the apex of the cochlea a minute orifice of communication between the two canals has been described by some writers, and doubted by others. According to Buck,* it is probable that no such opening exists in the natural condition of the parts, unless it be microscopic in size. But whether the canals communicate or not at this point, the partition between them is partly membranous throughout; and by this means any increase or diminution of pressure at the fenestra ovalis will be transmitted, through the scala vestibuli and scala tympani, to the membrane of the fenestra rotunda. This provides therefore for the movement of the stapes, notwithstanding the incompressible nature of the fluid of the labyrinth.

But the septum formed by the spiral lamina and membrana basilaris is not the only longitudinal partition in the cochlea. The scala vestibuli is also divided into two parallel canals, an internal and an external, by a thin membranous sheet, which starts from the upper surface of the spiral lamina near its outer border, and extends upward and outward to the external wall of the cochlear cavity. As this membrane leaves the spiral lamina at an angle of 45 or 50 degrees, it shuts off from the scala vestibuli a separate canal of prismatic form, having for its floor the membrana basilaris, for its outer wall the wall of the cochlea, and for its upper boundary the oblique membranous partition above described. This canal contains the auditory epithelium and the terminal fibres of the auditory nerve. It is therefore the essential part of the cochlea, and is termed the *ductus cochlearis*.

The ductus cochlearis terminates at its apex by a blind extremity; but at its base it communicates, by a narrow channel, with the cavity of the sacculus. It is consequently an extension of the sacculus, and part of the membranous labyrinth; while the scala vestibuli belongs to the general cavity of the vestibule. The ductus cochlearis may be considered as a tubular prolongation of the sacculus, rolled upon itself in a spiral form, and held in position by the adjacent parts of the cochlea. Like the rest of the membranous labyrinth, it is filled with a watery fluid, and surrounded by the perilymph, except where it is adherent to the walls of its bony cavity.

Organ of Corti.—The ductus cochlearis is lined with pavement epithelium, except along the middle of the membrana basilaris. Here there is a continuous elevated ridge, four or five times thicker than the epithelium elsewhere, consisting of enlarged and modified epithelium cells, and containing the terminal fibres of the auditory nerve. This body is named the *organ of Corti*,† from the observer by whom it was first described. It is justly considered as the most remarkable structure in the internal ear, although in its essential features analogous to the auditory spots of the sacculus and utricle.

The organ of Corti rests upon the upper surface of the membrana basilaris. Its framework consists of a series of elongated, rafter-like bodies, arranged in two rows, internal and external. These bodies, the

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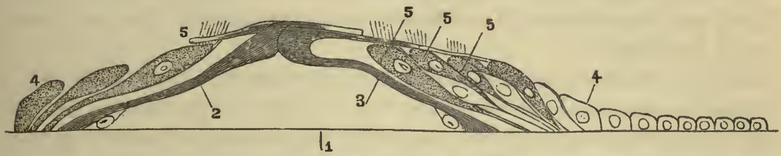
* On the Mechanism of Hearing. Prize Essay of the Alumni Association of the College of Physicians and Surgeons, New York. *New York Medical Journal*, June, 1874.

† Zeitschrift für wissenschaftliche Zoologie. Leipzig, 1851, Band iii., p. 109.

inner and outer "fibres of Corti," are separated below, where they rest upon the membrana basilaris, by a considerable interval; but their upper extremities lie in contact with each other, thus forming a roof-like connection, the "arch of Corti." Near the arch, the epithelium cells increase in length; and at its inner border there is a row of cells nearly as long as the innermost fibres of Corti, and in a similar leaning position, bearing upon their upper extremity a tuft of rigid hairs or cilia. On the outer border of the arch there are three such rows of hair cells; and in every instance the cilia project through openings in a sort of fenestrated cuticle extending above the cells, inward and outward, from the middle of the arch.

FIG. 152.



DIAGRAMMATIC SECTION OF THE ORGAN OF CORTI.—1. Membrana basilaris. 2, 3. Internal and external fibres of the arch. 4. Epithelium cells near its inner and outer borders. 5. Hair cells lying in contact with the arch. Magnified 500 diameters.

The fibres of the cochlear branch of the auditory nerve are distributed to the organ of Corti. The bundles forming this branch penetrate the base of the cochlea, and thence pass upward, through its axis, diverging successively in a horizontal direction between the two layers of the spiral lamina. At the attached border of the lamina, within the osseous canal, there is a linear collection of bipolar nerve cells, in and among which the fibres pass, and with many of which they are connected. This forms the "spiral ganglion" of the cochlear nerve. After the fibres have passed through this ganglion, they diverge toward the outer border of the spiral lamina and the membrana basilaris. At this point they diminish in size and lose their medullary layer; after which they penetrate into the ductus cochlearis, and reach the organ of Corti. In this organ their termination in the epithelial hair cells has been most positively described and figured by Waldeyer.* It evidently represents, in the ductus cochlearis, the especial apparatus of auditory sensibility.

Physiological Action of the Cochlea.—The cochlea, no doubt, as compared with the rest of the internal ear, serves for the precise discrimination of minute variations in sound. Its elongated and spiral form, the two membranes of uniform tension which inclose the ductus cochlearis, and the multiple rows of hair cells in the organ of Corti, all indicate its capacity for the distinct perception of sonorous impulses. Its analogy of construction, in some respects, with stringed musical instruments, has induced the belief, in many physiologists, that it is the

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* Stricker's Manual of Histology, Buck's edition. New York, 1872, p. 1040.

organ by which we appreciate the pitch of musical sounds. According to this view, the radiating fibres of the membrana basilaris are attuned, by their length and tension, to different notes of the musical scale; and the vibration of each is communicated to corresponding hair cells in the organ of Corti, thus reaching the terminal fibres of the auditory nerve. For every note which gains admission to the internal ear, only certain fibres and hair cells of the ductus cochlearis are thrown into vibration, and only certain fibres of the cochlear nerve receive a sonorous impression. There is certainly an apparent similarity between the fibrous and cellular elements in the organ of Corti and the ranges of strings, capable of vibrating to different notes, in a harp or pianoforte; and the similarity is sufficient to suggest a corresponding action in the two cases.

But the difficulty in attributing to the cochlea the discrimination of musical notes, lies in the fact that its development in different animals does not correspond with their capacity for the production and perception of musical sounds. The cochlea, under the form which it presents in man, is confined to the mammalia. In birds this part of the auditory apparatus is an obtusely conical eminence,* containing two small cartilaginous cylinders united by a membrane representing the membrana basilaris; and the part corresponding with the organ of Corti contains only nerve terminations and hair cells somewhat resembling those of the inner row in mammalia; the arch of Corti, and the three outer rows of hair cells, with their cuticular covering, being absent. In serpents and lizards, the cochlea is similar to that of birds; while in the naked reptiles and in fishes it is completely undeveloped.

Thus, in all the mammalia, the cochlea is an important part of the internal ear, but little inferior to the same organ in man. But in singing birds it is comparatively rudimentary. Some of these birds may be taught to repeat particular melodies, showing that their capacity of discriminating musical notes is equal to their power of producing them by the vocal organs. And yet that part of their auditory apparatus which should be most highly developed according to the view in question, is in reality the least so. If we compare a horse or a pig with a thrush or a mocking-bird, it is evident that the grade of musical sensibility in these animals is in no relation with the development of the cochlea. In fact, the cochlea of a singing bird resembles that of a crocodile or a serpent more closely than that of a quadruped or a man. At the same time, the other parts of the internal ear in birds, the double sac of the vestibular cavity, the membranous semicircular canals and ampullæ, the fenestra ovalis, and the fenestra rotunda, are all highly developed; some of them nearly or quite as much so as in mammalians.

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* Owen, Anatomy of the Vertebrates. London, 1866, vol. ii., p. 134. Wagner, Comparative Anatomy of the Vertebrate Animals, Tulk's Translation. New York, 1845, p. 95. Waldeyer, in Stricker's Manual of Histology, Buck's Edition. New York, 1872, p. 1046.

This throws a doubt on the special office of the cochlea in auditory sensations.

Persistence of Sonorous Impressions and the Production of Musical Sounds.—The effect produced by a sonorous vibration continues for a short time after the cessation of its cause. Usually the interval between two different impulses is sufficient to allow the first impression to disappear before the second is received, and the ear distinguishes them in succession. But if they follow each other at equal intervals, with a certain rapidity, they produce the impression of a continuous sound; and this sound has a higher or lower pitch, according to the rapidity of its vibrations. The numerical relation of musical notes thus produced has been studied by various means. One of these is the *siren* of Savart, in which successive puffs of air are emitted through small openings, with a rapidity which can be varied at will and registered by an automatic index. In another method the shocks are given by the points of a toothed wheel turning with known velocity against the projecting edge of a card. The number of vibrations corresponding to a particular note may also be registered by attaching to the extremity of a tuning-fork, a light stilet which traces upon the surface of a revolving cylinder, an undulating line (Fig. 96, *a*); the number of undulations in a given space indicating the frequency of vibration of the tuning-fork. A *simple* vibration represents the movement in one direction; a *double* vibration is the complete to-and-fro oscillation, which brings the moving point back to its original position.

By this means it is found that sonorous impulses, following each other with a rapidity of less than sixteen times per second, are separately distinguishable; but above that frequency they are merged into a continuous sensation. When the shocks are repeated at irregular intervals, the only characters perceptible in the sound are its intensity and quality. But if they succeed each other at regular intervals, the sound produced has a position in the musical scale, as a high or low note. The more frequent the repetitions, the higher the note; but a limit is at last reached at which the ear fails to perceive the sound, and an excessively high note is therefore inaudible. This is probably due to the following reason: A sonorous vibration, to be perceptible, must have a certain extent or amplitude; that is, the particles of the vibrating body must move to and fro, at each impulse, for a certain distance in space. The intensity of a sonorous impression, accordingly, depends on the amplitude of the vibrations, while its pitch or tone depends on their frequency. But the more frequently a body vibrates in a given time, the less extensive must be its movements, if their velocity remain the same. Consequently, when these vibrations arrive at a certain frequency, unless their velocity be increased in proportion, their amplitude becomes so small that they make no impression on the ear, and they are therefore inaudible.

It is evident, however, that such a sound would be perceptible if the sensibility of the auditory apparatus were increased to the requisite degree; and it is supposed that certain insects may be capable of perceiving sounds of very high pitch which are inaudible to the human ear. To an organ of such acute sensibility a very low note, on the other hand, would appear as a succession of distinct impulses.

The limits of frequency, within which sonorous vibrations are perceptible to man as musical sounds, are 16 double vibrations per second for the lowest notes, and 38,000 for the highest. But, according to Wundt, the exact discrimination of musical pitch is confined within much narrower limits, especially for the higher notes.

Duration of a Sound required for Sonorous Impressions.—This point has been investigated by Savart* in the following manner: He ascertained, by experiment, that the ear could appreciate the pitch of a sound made by a toothed wheel revolving at the rate of 10,000 shocks per second. By successively removing the teeth from different portions of its circumference, he diminished in a corresponding degree the time during which the shocks were produced; and he found that such a wheel would give a sound of definite pitch with only two teeth adjacent remaining. The double shock thus produced would occupy only $\frac{1}{5000}$ of a second; and this duration of impulses was sufficient to make upon the ear a distinct musical impression.

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* Daguin, Traité Elémentaire de Physique. Paris, 1869, tome i., p. 517.

SECTION IV.

REPRODUCTION.

CHAPTER I.

THE NATURE OF REPRODUCTION AND THE ORIGIN OF PLANTS AND ANIMALS.

REPRODUCTION is the process by which the different kinds of organized beings are perpetuated, notwithstanding the limited existence of each individual. It includes the production, growth, and development of new germs, as well as the history of successive changes in the organs and functions, and the modifications of external form at different periods of life.

All organized bodies pass through various stages of development, in which their structure and functions undergo corresponding alterations. The changes of nutrition and growth, by which the animal or plant is distinguished, correspond in activity with its other vital phenomena; since these phenomena depend on the continuance of the nutritive process. Thus the organs and tissues are the seat of a double change of renovation and decay, but retain nevertheless their original constitution, and continue to exhibit their vital phenomena.

This change, however, is not the only one which takes place. Although the bodily structure appears to be maintained by the nutritive process from one moment to another, or from day to day, yet examination at longer intervals will show that this is not precisely the case; since the changes of nutrition are progressive as well as momentary. The composition and structure of the bones are not the same at the age of twenty-five years that they were at fifteen. At the later period they contain more calcareous and less organic matter than before; their solidity being consequently increased, while their elasticity is diminished. There is a notable difference in the quantities of oxygen and carbonic acid inspired and exhaled at different ages; and the irritability of the muscles is diminished after some years, owing to a slow, but steady and permanent, deviation in their intimate constitution.

The vital properties of the organs, therefore, change with their varying structure; and a time comes at last when they are perceptibly less capable of action than before. The very exercise of the vital powers is inseparably connected with the alteration of the organs to which they belong; and the functions of life, instead of remaining indefinitely the same, pass through a series of changes, which finally terminate in their complete cessation.

The history of an animal or plant is, therefore, a history of successive epochs or phases of existence, in each of which its structure and functions differ more or less from those in every other. The organized being has a definite term of life, through which it passes according to an invariable law, and which, at some regularly appointed time, comes to an end. The plant germinates, grows, blossoms, bears fruit, withers, and decays. The animal is born, nourished, and brought to maturity, after which he retrogrades and dies. The very commencement of existence, by leading through its successive intermediate stages, conducts at last necessarily to its termination.

But while individual organisms are constantly perishing and disappearing from the stage, the particular kind, or *species*, remains in existence, without any important change in the forms belonging to it. The horse and the ox, the oak and the pine, the numerous wild and domesticated animals, as well as the different races of mankind, have remained without essential alteration since the earliest historical epochs. Yet during this period innumerable individuals, of each species or race, have lived through their natural term and successively passed out of existence. A *species* may therefore be regarded as a type or class of organized beings, in which the individuals composing it die off and disappear, but which nevertheless repeats itself from year to year, and maintains its ranks constantly full by the continued accession of other similar forms. This process, by which new organisms make their appearance, in place of those which are destroyed, is the process of *reproduction*. The first important topic, in the study of reproduction, is that of the conditions necessary for its accomplishment.

Reproduction by Generation.

It is well known that, in the reproduction of animals or plants, the young organisms are produced, as a rule, from the bodies of the elder. The relation between the two is that of parents and progeny. The progeny, accordingly, owes its existence to an act of *generation;* and the new organisms, thus generated, become in turn the parents of others which succeed them. For this reason, wherever such plants or animals exist, they indicate the preceding existence of the same species; and if by any accident the whole species should be destroyed in any particular locality, no new individuals could be produced there, unless by the importation of others of the same kind.

The most prominent feature of generation, as a natural phenomenon, is that the young animals or plants thus formed *are of the same kind with their parents.* They reproduce the specific characters by which their predecessors were distinguished; and this takes place by a law so universal that it seems almost a truism to state it. But this is only because it has been so constantly a matter of observation, that in popular experience it appears a natural necessity. In reality it is one of the most remarkable phenomena connected with the generative process; and it indicates an unbroken connection of physiological acts, extending through the lives of many different individuals. Thus we know that the progeny of a fox will always be foxes; and that if we sow oats, it will be a crop of oats that is produced in consequence. Generation, accordingly, not only gives rise to new animals or plants, but it serves to continue indefinitely the existence of the species, with its characteristic marks and qualities.

Our idea, therefore, of a species includes two different elements, one of which is anatomical, the other physiological. Its anatomical character is the similarity of form, size, and structure between the individuals belonging to it, which we recognize at a glance; its physiological character is the fact, established by experience, that it will reproduce itself, and thus remain distinct through an indefinite series of successive generations.

It is not possible to say that the anatomical characters of a species have been absolutely the same throughout all previous time, or that they will remain so without limit in future. The fossil remains of animals and plants, differing from those now in existence, show that species are not persistent and invariable through very long periods; and that they may either become so modified as to present a different appearance, or may entirely come to an end, like the extinct mastodons and horses of the United States, and be replaced by others from a different locality. But in whatever way we may explain the geological succession of different species, it is certain that at any one time their essential characters are those above described; and that each species, by the process of generative reproduction, remains distinct from the others which are contemporary with it.

But the production of young animals, similar to their parents, although the final result of the generative process, is never immediate. The young progeny is at first different from its parents, and only comes to resemble them through a series of changes, often very remarkable in kind. The embryo of a vertebrate animal, though incomplete in structure, presents some analogy of form with the adult. But in many invertebrates, the young, even when hatched and capable of active locomotion, are so different from their parents that they would never be referred to the same species, unless their identity were demonstrated by subsequent development. The young mosquito is a wingless creature living beneath the surface of stagnant pools; and the eggs of the butterfly, when hatched, give birth not to butterflies but to caterpillars. The caterpillars, however, are not creatures of another species, but young butterflies; and they become similar to their parents after certain changes, which take place at definite periods of their development.

The reproduction of form, therefore, which marks a species, is accomplished through a series of changes in regular order; and this series, taken together, may be represented by a circuit, which starts from the egg, is continued through successive phases of growth, transformation and maturity, and terminates at last with the production of an egg. As this egg is similar to the first, the changes repeat themselves in their previous order, and the indefinite continuance of the species is thus established.

Spontaneous Generation.—The commonest observation shows that the above facts hold good in regard to all animals and plants with whose history we are fully acquainted. But it has sometimes been surmised that there are exceptions to this rule; and that living beings may, under certain circumstances, be produced from inanimate materials; thus presenting the singular phenomenon of a progeny without parents. Such a production of organized bodies is known as *spontaneous generation.* Its existence is doubted by most physiologists, and has never been positively established for any particular species; but it has been at various times the subject of discussion, forming a somewhat remarkable chapter in the history of physiology.

It may be remarked in general that the organisms, supposed capable of originating by spontaneous generation, have been always those whose natural history was obscure, owing either to their minute size or to certain physiological peculiarities. Wherever animals or plants appeared in abundance without evidence of the source from which they came, it was formerly conjectured, for that reason, that their production was spontaneous; and the ancient naturalists supposed all animals, except those which visibly lay eggs or produce living young, to be formed by the fortuitous combination of their organic ingredients. Maggots, shell fish, grubs, worms, and even some fishes were thought to be produced in this way, because they had no apparent specific origin.

But further observation showed that these animals were really produced by generation from parents; their secret methods of propagation being discovered, and their relationship being detected by following the development of the young. A frequent obstacle to the identification of species, in these investigations, is the interval which elapses between the laying of the eggs and the subsequent appearance of the young brood; the new generation not showing itself until the former has disappeared. A striking instance is that of the seventeen-year locust (*Cicada septendecim*), where a period of seventeen years intervenes between the hatching of the larva and the appearance of the perfect insect; the larva all this time remaining buried in the ground, while the life of the perfect insect does not last over six weeks. But notwithstanding this difficulty, most of these cases were gradually traced to the usual method of generation from parents.

Another source of error is the dissimilarity sometimes existing between parents and young, especially when accompanied by a difference in their habits of life. Until the middle of the seventeenth century there was no more undoubted instance of spontaneous generation than the appearance of maggots in putrefying flesh. These creatures always show themselves in meat at a certain stage of its decomposition; they are never seen elsewhere; and they do not apparently possess the power of producing young. For these reasons they were believed to originate from the dead flesh and to die without leaving a progeny. But the experiments of Redi in 1668, demonstrated the fallacy of this opinion and the true origin of the maggots. He took, in the month of July, eight wide-mouthed bottles and placed in them pieces of flesh. Four of the bottles were left open to the atmosphere, while the remaining four were closed by paper fastened over their orifices. In a short time the flesh in the uncovered bottles was filled with maggots, a peculiar kind of fly meanwhile passing in and out by the open mouth; but in the closed bottles not a maggot was visible, even after several months.

Thus it was evident that the maggots were not formed from the dead flesh, but that their germs came in some way from without; and continued observation showed that they were hatched from eggs deposited by the flies, and that after a time they became perfect insects similar to their parents. An extension of these observations to other invertebrate animals made known a great variety of instances in which the connection of parents and progeny might be traced through several intermediate conditions; so that apparent differences in their configuration and structure no longer offered a serious difficulty to the investigator. As a general rule, since that time, whenever a rare or comparatively unknown animal or plant has been suspected to originate by spontaneous generation, it has only been necessary to examine thoroughly its habits and functions, to discover its real methods of propagation, and to show that they correspond, in all essential particulars, with the ordinary laws of reproduction. The limits within which the doctrine of spontaneous generation could be applied have been thus gradually narrowed, in the same degree that the study of natural history has advanced; the presumption of its existence always hanging upon the outskirts of definite knowledge, and relating only to those animals or plants which are for the time imperfectly understood. The two groups from which it has been most recently excluded are the Entozoa and the Infusoria.

I. *Entozoa.*—These are parasitic organisms inhabiting the bodies of other living animals, from whose organic juices they derive their nourishment.

There are many kinds of entozoa, all of which are confined, more or less strictly, to certain parts of the body which they inhabit. They are found in the intestines, the liver, the kidneys, the lungs, the heart, and the blood-vessels; some on the surface of the brain; others in the muscles or in the eyeball. Each parasite, as a rule, is peculiar to the species of animal which it inhabits, and to a particular part of the body, or even to a part of one organ. Thus, Ascaris lumbricoides is found in the small intestine, Oxyuris vermicularis in the rectum, Trichocephalus dispar in the cæcum. One kind of Distoma has its place in the lungs of the green frog, another in those of the brown frog. Cysticercus cellulosæ is found in the connective tissue; Trichina spiralis in the substance of the muscles.

With regard to many of these parasites the only difficulty in accounting for their existence, otherwise than by spontaneous generation, lay in their being confined to such narrow limits. It seemed probable that some local conditions must be requisite for the production of a parasite, which was only to be found in the biliary passages, the kidneys, or the lungs of a living animal. A little consideration, however, makes it evident that these conditions are neither necessary nor sufficient for the *production* of such a parasite, but only for its development and nutrition. Most internal parasites reproduce their species by generation. They have male and female organs, and produce fertile eggs, often in great abundance. The eggs in a single female Ascaris are to be counted by thousands; and those in a tapeworm by millions. In order that these eggs may be hatched, and their embryos developed, certain conditions are requisite; as the seeds of plants need, for their germination and growth, an appropriate soil and a certain degree of warmth and moisture. It is no more remarkable that Oxyuris vermicularis should inhabit the rectum, and Ascaris lumbricoides the ileum, than that Lobelia inflata should grow only in dry pastures, and Lobelia cardinalis by the side of running brooks. The lichens flourish on the exposed surfaces of rocks and stone walls; while the fungi vegetate in darkness and moisture, on the decaying trunks of dead trees. Yet all these plants are reproduced by generation, from germs which require special conditions for their growth and development. If any animal or vegetable germ be deposited in a locality where the requisite conditions are present, it is developed and comes to maturity; otherwise not. Thus the internal parasites, like other living organisms, are confined to certain situations by the necessities of their nourishment and growth.

But in some instances there are two further difficulties. First, the parasites in question do not inhabit the open passages or canals of the body, but lie encysted, in the solid substance of the tissues, without visible means of access from the exterior. Secondly, they are sexless; and, if they perform no generative function, it does not readily appear how they can themselves have been derived from parents. The two kinds of entozoa, in which these peculiarities are most strongly marked, and in which they have been must fully explained, are Cysticercus cellulosæ and Trichina spiralis.

1. *Cysticercus cellulosæ.*—This is a bladder-shaped parasite of somewhat flattened form, about 10 millimetres in diameter, found in the subcutaneous and intermuscular connective tissue of the pig, where it appears under the form of whitish specks, giving rise to the appearance known as "measly pork." Each parasite is enveloped in a cyst, but the bladder-like body, when extracted, exhibits at one spot a minute

depression or involution of its wall. From this point a slender neck, ending in a rounded head, may be extruded by pressure; after which the animal is seen to consist of a head and neck, terminated posteriorly by a dilated, sac-like tail, whence its generic name of cysticercus. Its specific name is derived from its inhabiting the connective tissue, formerly known as the "cellular tissue." The head of the parasite, when magnified, shows upon its surface four sucking disks, and near its extremity a double crown of curved calcareous processes or hooks. There are no distinguishable internal organs, and the caudal vesicle contains only an albuminous fluid. Thus there is no other apparent source for these organisms than the tissues which they inhabit, nor have they any visible mode of continuing their species by generation.

Fig. 153.

Cysticercus Cellulosæ, from the flesh of the pig. Natural size.—1. Vesicular appendage, with the head and neck extruded. 2, 3. The same, with head and neck inverted; viewed in different positions. (Davaine.)

But it has been shown by Van Beneden, Leuckart, Haubner, and Küchenmeister,* that Cysticercus cellulosæ is the embryonic progeny of Tænia solium, or the solitary tapeworm, found in the small intestine of man. The specific identity of the two was first suspected from the similarity of the head, which presents the same sucking disks and crown of hooks in Tænia as in Cysticercus. But in Tænia the neck, instead of terminating in a vesicular appendage, is elongated and wrinkled. The wrinkles, after a certain distance, become deepened into superficial furrows, marking off the body into oblong articulations, each articulation showing a double system of communicating vascular canals, and distinctly-marked generative organs of both sexes. As they recede by successive growth farther from the head, the generative organs become more complete, and are at last filled with mature fecundated eggs, in which the embryos are already partially developed. The tapeworm then forms a chain or colony of articulations, sometimes from six to eight metres in length, attached to the mucous membrane of the intestine by the minute head at its anterior extremity.

By the experiments above mentioned it was found: 1st. That mature articulations from the tænia solium of man, if administered to young pigs with their food, produce a brood of cysticercus cellulosæ in the flesh of these animals; and, 2d. That cysticercus cellulosæ from measly pork, if swallowed by man, becomes developed in the intestine, within a few days, into ribbon-like worms, recognizable as young specimens of tænia solium.

The manner in which the pig becomes infested with cysticercus is as follows: In the fully-formed tapeworm, in the human intestine, the mature articulations separate from the rest of the colony, and either

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* Animal and Vegetable Parasites. Sydenham edition, London, 1857, pp. 115, 120.

find their way out singly by the anus, or are discharged with the evacuations. They have, while living, considerable power of contractility and locomotion; and thus become transferred to neighboring vegetable substances, which are devoured by the pig. In the pig's stomach and intestine, the substance of the articulation is digested; but the embryos, which are but little over 30 mmm. in diameter, and armed with movable calcareous spines, make their way through the intestinal walls, and are thence dispersed, either by active locomotion or by the circulating blood, throughout the connective tissue. Here they become encysted, and go through with a partial development, until they acquire the form of cysticercus. In this condition they remain until the flesh of the pig is used for food, when they are transformed, as above described, into tænia solium, thus reproducing the original form of the parasite. A similar relation has been found by Küchenmeister and Siebold between certain other species of tænia and cysticercus.

2. *Trichina spiralis.*—This is an encysted, worm-like parasite, found in the muscular tissue of the pig, and sometimes in that of the rat, the cat, and the human species. Each worm lies spirally coiled within its enveloping cyst. It is about 0.75 millimetre in length, with a tapering anterior and a rounded posterior extremity. It has a nearly straight intestine and rudimentary sexual organs. It has long been recognized as an occasional parasite in the muscular tissue of man; but it is only since the investigations of Leuckart* and Pagenstecher† that the history of its growth and development has been made known. If muscular flesh containing encysted trichinæ be administered to a rabbit, cat, rat, mouse, or pig, the cysts are digested and the worms liberated in the intestine. Here they rapidly increase in development; the females becoming impregnated and filled with living young, and attaining, at the end of a fortnight, three or four times their previous size. The embryos are now discharged into the cavity of the intestine; after which they penetrate the intestinal walls, and thence disperse throughout the body. On reaching the muscular tissue, they become encysted, and thus remain quiescent until introduced into the intestine of another animal or of man. The existence of such sexless and encysted parasites is therefore analogous to that of the caterpillar or the maggot. They are sexless, because they are still in the embryonic condition. But they have been produced by generation from parents; and they will, at a subsequent period, themselves produce young by the same process.

FIG. 154.

TRICHINA SPIRALIS, encysted, from muscular tissue of a trichinous cat. Magnified 76 diameters.

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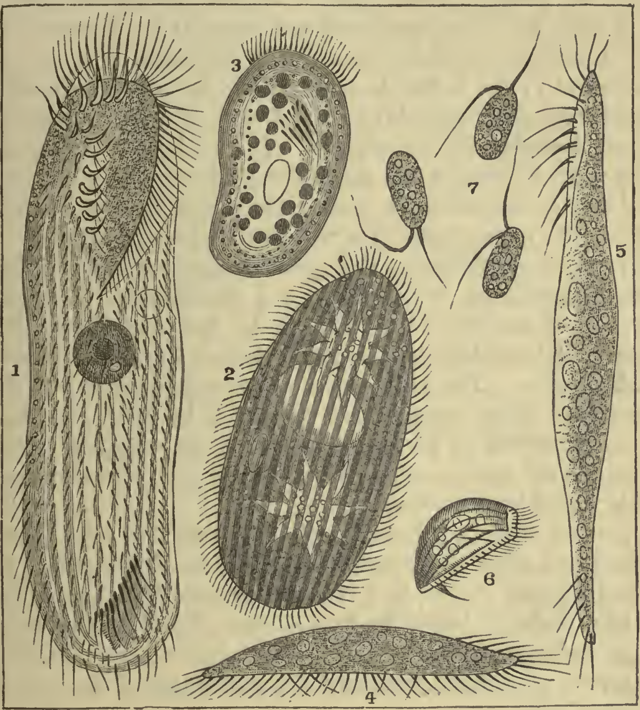
* Untersuchungen über Trichina spiralis. Leipzig und Heidelberg, 1860.

† Die Trichinen. Leipzig, 1866.

II. *Infusoria.*—These are microscopic organisms, first discovered by Leeuwenhoek, in 1675, in rain-water which had been kept in standing vases. On account of their active movement and minute size he called them "animalcules;" but as they were soon found to make their appearance in great numbers and with remarkable rapidity in watery infusions of organic matter exposed to the air, they afterward received the general name of "infusoria." They present themselves under a great variety of forms; so much so that Ehrenberg* described more than 700 different kinds. They are generally provided with cilia attached to the surface of their bodies, and are, for the most part, in constant and rapid motion in the fluid which they inhabit.

Fig. 155.



INFUSORIA, of various kinds.—1. Urostyla grandis, from decaying sedge-grass. 2. Paramecium aurelia, from vegetable infusions. 3. Chlamydodon mnemosyne, Baltic Sea water. 4. Kerona polyporum, on the fresh-water polype. 5. Oxytricha caudata, open stagnant waters. 6. Ervilia fluviatilis, clear brook water. 7. Heteromita ovata, on aquatic river plants. Magnified 325 diameters. (Ehrenberg and Stein.)

In consequence of the numerous forms of the infusoria, their frequent changeability of figure, and their want of resemblance to any previously known organisms, they were thought, by some earlier observers, to have no regular mode of generation, but to arise indis-

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* Die Infusionsthierchen als vollkommene Organismen. Leipzig, 1838.

criminately from the organic materials of the infusion; the particular form which they might assume in any case being determined by the physical conditions present. Their inevitable appearance in organic infusions, under ordinary temperatures and exposures, contributed to this belief. The substance of the infusion might be previously baked or boiled; the water in which it was infused might be purified by distillation from all organic contamination; and yet infusoria would make their appearance at the usual time and in the usual abundance, provided the infusion were exposed to moderate warmth and to the access of air. But these conditions are essential to all organic life, and are not, therefore, especially requisite for infusoria.

Consequently, the infusoria must either have been spontaneously generated from the materials of the infusion, or else their germs must have been introduced from without In the latter case these germs must be wafted about by the atmospheric currents, in a comparatively dry and inactive condition, to resume their development when brought in contact with moisture and the requisite organic material.

The researches relating to this question continued from 1775, when they were carried on by Needham and Spallanzani, throughout the greater part of the present century, in the hands of Cuvier, Schultze, Helmholtz, Milne-Edwards, Longet, Pouchet, Pasteur, Wyman, Tyndall, and Bastian. The main object of investigation was to discover, if all previous living germs were destroyed by heat, and the access of others prevented by hermetically sealing the vessels or thoroughly purifying the air introduced, whether, under such circumstances, infusorial life would be developed.

The general result of these experiments was that such precautions diminished and often prevented the production of infusoria. Spallanzani* had already shown, in 1776, that organic infusions in hermetically sealed flasks, if boiled for two minutes, failed to produce any of the larger and more highly organized animalcules; and that boiling for three-quarters of an hour prevented the appearance of the more minute and simpler kinds.

Schultze† performed similar experiments, with the addition of admitting to the organic infusion purified air. He placed his infusion in a glass flask, the stopper of which was provided with two narrow tubes, bent at right angles. When the infusion had been thoroughly boiled, and all air expelled from the flask by the vapor of ebullition, he fastened to each tube a series of bulbs containing on one side sulphuric acid, and on the other a solution of potassium hydrate; so that the air which reëntered the flask while cooling must pass through these fluids, and thus be cleansed of all living organic matter. The apparatus was then kept in a warm place for two months, during which time the air was renewed daily by suction through the tubes, without any infusoria being

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* Opuscoli de Fisica animale e vegetabile. Modena, 1776, vol. i., p. 10.

† Poggendorf's Annalen, 1836. Band xxxix., p. 487.

detected in its contents. But they showed themselves in abundance after the flask had been opened, and the infusion exposed for a few days to the direct access of air.

Pasteur* found that if a flask containing an organic infusion were boiled upon a high mountain, where the air is of unusual purity, allowed to fill itself with this air while cooling, and then hermetically sealed, it would often remain free from infusorial growth. Several such flasks, boiled and filled with air on the Montanvert in Switzerland, were kept for four years, without their contents undergoing any perceptible change. But on making, at the end of that time, a minute opening in the neck of one flask, the infusion exhibited after three days a perceptible growth of cryptogamic vegetation.

These results did not absolutely exclude the possibility of spontaneous generation, which was still maintained by Pouchet and other observers; but they indicated the existence of atmospheric germs, capable of development in a suitable organic infusion.

But in the mean time the study of the infusoria had been going on independently of the question of spontaneous generation, and had been sufficient to demonstrate their reproduction in the usual way, by fertilized eggs and embryonic development.

The apparent confusion and variability in form of the infusoria, at the time of their first discovery, depended largely on their great numbers and imperfect knowledge of their natural history. Subsequent observation has shown their organization to be as definite as that of other classes of the animal kingdom; and they have now been arranged, by the labors of Claparède and Lachmann,† Stein,‡ and Balbiani,§ in orders, families, genera, and species, which may be recognized with certainty by their distinctive marks. They are not confined to infusions of decaying material; but many have their natural habitation in lakes, pools, marshes, running brooks, or the open sea. Certain forms, originally included in this class, such as Rotifer, Stephanoceros, and Floscularia, have been found to possess a more complicated structure than the rest, and to belong properly to the class of worms; their mode of reproduction being sufficiently manifest from the fact that they often contain living embryos, in process of development.

Finally, the true ciliated infusoria have also been shown to reproduce their species by means of eggs, formed in special generative organs and fecundated by union of the sexes (Fig. 156). This fact, first demonstrated by Balbiani, has been since confirmed, in numerous instances, by Stein, Engelmann,‖ and Cohn;¶ Balbiani and Stein together having

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* Comptes Rendus de l'Académie des Sciences. Paris, Février 20, 1865.

† Etudes sur les Infusoires et les Rhizopodes. Genève, 1856–1861.

‡ Organismus der Infusionsthiere. Leipzig, 1859.

§ Journal de la Physiologie de l'Homme et des Animaux. Paris, 1861.

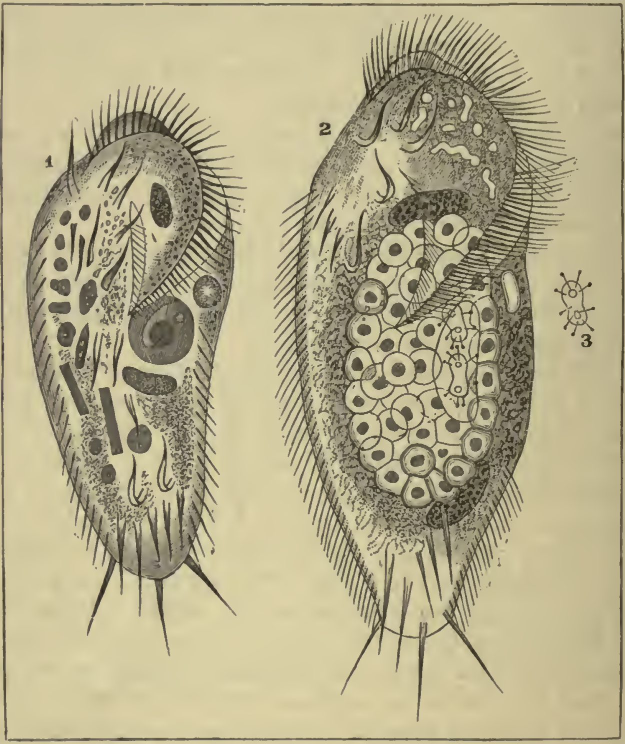
‖ Zeitschrift fur wissenschaftliche Zoologie. Leipzig, 1862, Band xi., p. 347.

¶ Ibid. Band xii., p. 197.

observed the occurrence of sexual generation in 47 different genera and 66 different species.

Thus the infusoria are in turn excluded from the field of spontaneous generation. But, on the other hand, a considerable group of organisms, formerly referred to this class, are now known to be of a different character. These are the forms included under the general term of *Bacteria*, and comprising the varieties of bacterium, vibrio, spirillum, and micrococcus. They are of a vegetable nature, notwithstanding their frequent exhibition of active movement; and they consist of cells, which multiply, often with great rapidity, by repeated subdivision. Whether they are also reproduced by germs, has not been determined; but their minute size and imperfect classification have thus far proved obstacles to the complete study of their physiological characters.

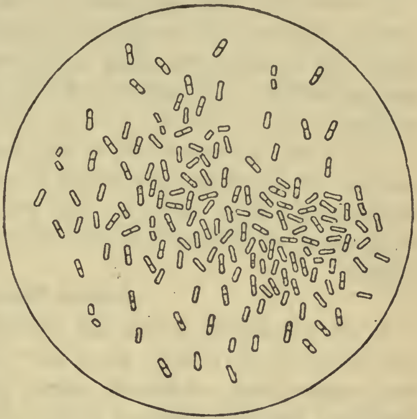
Fig. 156.



Stylonychia Mytilus; a fresh-water infusorium.—1. Unimpregnated. 2. Impregnated, and containing mature eggs and two embryos. 3. Showing the form of the embryo. Magnified 375 diameters. (Stein.)

The representative of this group is the species known as *Bacterium termo*, already described (page 78), in connection with the phenomena of putrefaction. It consists of rod-like cells, averaging 3 mmm. in length by 0.6 mmm. in thickness, sometimes single, often double, two of them being attached, end to end. The latter appearance is due to their multiplication by transverse division, which takes place at the middle of their length. The two new cells thus produced remain for a time in connection with each other, and afterward separate, to repeat the process independently. During a considerable part of their existence, the cells are in rapid vibratory and progressive movement. The vibrations take place in a circular manner, about a point situated at or near one of the extremities; so that the rest of the cell performs a conical movement around this point, presenting, on superficial examination, the appearance of lateral oscillation. The mechanism by which this movement is accomplished is unknown; but it is no doubt analogous to the slower spiral undulations of the *Oscillatoriæ*, among fresh-water algæ; and its effect is to propel the bacterium cells, often with extreme velocity, through the fluid in which they are immersed.

Fig. 157.



CELLS OF BACTERIUM TERMO; from a putrefying infusion.

Of late years, the investigations in regard to spontaneous generation have been mainly confined to bacteria and their allies, since they now form the only group of organisms in which reproduction by generation has not been established. Even for them, the rapid multiplication by cell division, which takes place under favorable conditions, indicates their usual mode of increase; but in order to establish an entire similarity between them and other living organisms, they must also be shown to reproduce by spores or germs, which thus far has not been done. The experiments with boiled infusions in sealed flasks have led to results which are not interpreted in the same manner by all writers; but it is evident that for bacteria, as well as for other organic forms, the application of heat exerts in various degrees a preventive action on their subsequent appearance.

The experiments of Wyman* on this subject were performed with animal and vegetable infusions, which, after being enclosed in sealed flasks, with atmospheric air, were immersed in boiling water for periods varying from thirty minutes to five hours, and afterward kept under observation at temperatures favorable for the development of bacteria. The result showed that the appearance of these organisms was always delayed by the application of a boiling heat, and that this delay was

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* American Journal of Science and Arts. New Haven, vol. xliv., September, 1867.

often in direct proportion to the length of the boiling process. Furthermore, in certain cases the bacteria failed to be produced at all, and the chance of their production was found to decrease in proportion to the time during which the liquid had been boiled. Thus, of four series of flasks, containing the same infusion, and boiled respectively for one, two, three, and four hours, all of the first and second series produced bacteria, only one of the third, and none of the fourth. Finally, in no instance, among numerous trials, did they appear in any infusion which had been boiled for a period exceeding five hours. Thus a limit was reached to the production of bacteria, in fluids previously subjected to the action of heat.

There can be no doubt as to the bearing of these and similar experiments. Spontaneous generation is inadmissible at the present day for everything except bacteria; and with regard to them there is no sufficient proof of their production independently of previously existing germs.

Sexual Generation.

In all the higher plants and animals generation is accomplished by the union of the sexes. Each sex is distinguished by special generative organs, male or female, which give rise to a peculiar organized product; and this product unites with that from the opposite sex, to form a new individual. The female organs produce an *egg* or *germ* capable of being developed into the young animal or plant; the male organs produce the *sperm* or *spermatic fluid*, necessary to fecundate the germ and communicate to it the stimulus of development.

In flowering plants, the female product is the "germ;" which, after fecundation by the male product or "pollen," becomes the seed or fruit, and may produce a new plant by further development. In many species, as in the lily, the violet, the convolvulus, both male and female organs are contained in the same flower; in some there are separate male and female flowers on the same plant, as in the oak, beech, birch, and hickory; and in others, as in the willow, poplar, and sassafras, the male and female flowers are on different plants of the same species.

In animals the female organs produce the "ovum" or egg, and are called *ovaries.* The male organs, which give rise to the spermatic fluid, are the *testicles.* In some invertebrate species, as in the snail, slug, leech, and earthworm, both ovaries and testicles are present in the same individual. But impregnation is nevertheless effected by the sexual union of two organisms; the eggs produced by one animal being fecundated by the seminal fluid of another, and *vice versâ.*

In all vertebrate animals, the two sets of generative organs are located in separate individuals; and the species is divided into two sexes, male and female. There are also, for the most part, accessory organs of generation, which assist in the accomplishment of the process, and occasion a corresponding difference in the bodily form. In some cases this difference is so great that the male and female would never be recognized as belonging to the same species, unless they were seen in company with each other, and were known to reproduce by sexual congress. Not to mention some extreme instances of this among insects and other invertebrate animals, it is sufficient to refer to the cock and the hen, the lion and the lioness, the buck and the doe. In man, the distinction shows itself in the mental constitution, the disposition, habits, and pursuits of the two sexes, as well as in the general conformation of the body, and its external appearance.

The special details of the generative process depend on the structure of the male and female organs, the manner in which the sexual products are formed and discharged, their union in the act of fecundation, and the changes which take place in the development of the embryo.

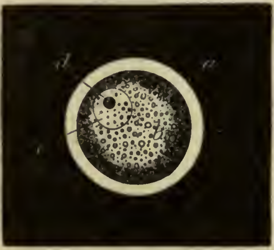
CHAPTER II.

THE EGG, AND THE FEMALE ORGANS OF GENERATION.

THE egg, in man and mammalians, is a globular body, about 0.25 millimetre in diameter. It consists of an external closed sac, the *vitelline membrane*, containing in its interior a spherical mass, the *vitellus*. Of these two, the vitellus is the essential part of the egg, since from its substance the rudiments of the embryo are formed. The vitelline membrane is a protective envelope, serving to maintain the form and integrity of the vitellus.

Vitelline Membrane.—The vitelline membrane is a smooth, transparent, colorless layer, about 0.01 millimetre in thickness. With a magnifying power sufficiently moderate to include a view of the whole egg, it presents a perfectly homogeneous aspect; although with higher powers, according to Klein, it exhibits an appearance of vertical striation. Notwithstanding its delicacy and transparency, it is very elastic, and has a considerable degree of resistance. If the mammalian egg be placed under the microscope, surrounded by fluid and covered with a thin glass, it may be perceptibly flattened by pressure; and when the pressure is removed it resumes its globular form. When slightly compressed in this way, the apparent thickness of its vitelline membrane is increased, giving it the appearance of a rather wide, pellucid border or zone, surrounding the granular and comparatively opaque vitellus. From this circumstance it has received the name of the "zona pellucida."

Fig. 158.



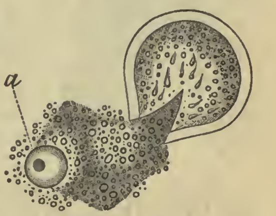
Human Ovum, magnified 75 diameters.—*a.* Vitelline membrane. *b.* Vitellus. *c.* Germinative vesicle. *d.* Germinative spot.

In the vitelline membrane of many invertebrates, and also in that of fishes, a minute opening has been discovered, termed the "micropyle," leading into its cavity; and through this opening the spermatic filaments of the male reach the vitellus. Such an opening may also exist in the vitelline membrane of other vertebrate animals; but the globular form of the egg, the homogeneous texture of the vitelline membrane, and the absence of any other material, of different refractive power, in the orifice of the micropyle, are obstacles to its detection under the microscope.

Vitellus.—The vitellus is a globular, semifluid, tenacious mass composed of transparent and colorless albuminous material, with oleaginous-looking granules thickly disseminated throughout its substance. Owing to the admixture of these two constituents, it has a granular aspect, and a considerable degree of opacity. Imbedded in the vitellus, near its surface, and consequently almost immediately beneath the vitelline membrane, is a clear, colorless, transparent, rounded sac—the *germinative vesicle.* In the mammalian egg, this vesicle measures about .04 millimetre in diameter. It presents upon its surface a nucleus-like spot, known as the *germinative spot.* Both the germinative vesicle and the germinative spot are partially concealed, in the uninjured condition of the egg, by the granules of the surrounding vitellus.

If the egg, while under the microscope, be ruptured by pressure on the cover-glass, the vitellus is gradually expelled by the elasticity of the vitelline membrane. It retains the granules imbedded in its substance, but the germinative vesicle often becomes detached, and therefore more distinctly visible.

Fig. 159.



Human Ovum, ruptured by pressure, showing the vitellus partially expelled, the germinative vesicle, with its germinative spot, at *a*, and the smooth fracture of the vitelline membrane.

In man and mammalians, the simple form of egg above described is sufficient for the production of the embryo, since it is retained, after fecundation, within the generative passages, and there absorbs the nutritious materials for its subsequent growth. In the naked reptiles and in most fish, where the eggs are deposited and hatched in water, the vitellus is also of small size; since the hatching takes place at an early period of development, and the requisite additional fluid is supplied from the surrounding medium. But in birds and most of the scaly reptiles, as serpents, turtles, and lizards, the eggs are deposited in a nest or in the ground, with no external source of nutrition for the embryo. In these instances the vitellus, or "yolk," is of large size; and the bulk of the egg is further increased by the addition, within the generative passages, of albuminous material and fibrous or calcareous envelopes.

Ovaries and Oviducts.—The eggs are produced in the interior of certain organs, situated in the abdominal cavity, called the *ovaries.* These organs consist of a mass of vascular connective tissue, inclosing numerous globular sacs or follicles, the "Graafian follicles;" so called from the anatomist* who first fully described them as constituent parts of the ovary. Each Graafian follicle contains an egg, which varies more or less in size and appearance in different classes of animals, but which has always the same essential characters, and is produced in the same way.

The egg thus grows in the ovarian sac, like a tooth in its follicle; and forms, accordingly, a constituent part of the body of the female. It is subsequently separated from its attachments, and thrown off; but

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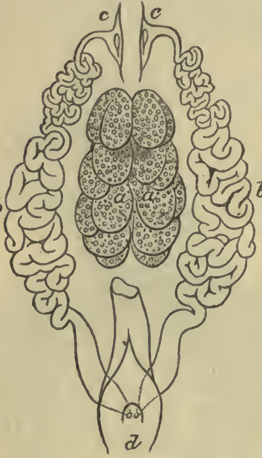
* Regner de Graaf, Opera Omnia. Amstelædami, 1705, p. 228.

until that time, it is one of the elements of the ovarian tissue, and is nourished like any other portion of the female organism.

Since the ovaries are directly concerned in the production of the egg, they form the essential part of the female generative apparatus; but in most instances there are also accessory organs, which take part in the process of generation. The most important are two symmetrical tubes, or *oviducts*, destined to receive the eggs from the ovaries and convey them to the external generative orifice. The mucous membrane of the oviducts is usually adapted for supplying certain secretions during the passage of the egg, which complete its formation or provide for the nutrition of the embryo.

Fig. 160.



Female Generative Organs of Frog.—*a. a.* Ovaries. *b. b.* Oviducts. *c. c.* Their upper orifices. *d.* Cloaca, showing lower orifices of oviducts.

In the frog, the oviduct commences at the upper part of the abdomen, by a rather wide orifice, communicating with the peritoneal cavity. It then contracts to a narrow tube (Fig. 158), folded upon itself in numerous convolutions, until it opens, near its fellow of the opposite side, into the "cloaca" or lower part of the intestinal canal. This is also the general character of the oviducts in nearly all reptiles and birds.

The ovaries, as well as the eggs which they contain, undergo at certain seasons a periodical development. In the frog, during the latter part of summer and in autumn, the ovaries appear like clusters of nearly colorless eggs, the smaller of which are perfectly transparent and less than 0.18 millimetre in diameter. But in early spring, the ovaries enlarge to four or five times their former size, becoming lobulated masses, crowded with dark-colored opaque eggs, each two millimetres in diameter. At the generative season, in all animals, a certain number of eggs, which were previously imperfect, increase in size and become altered in structure. The vitellus especially, at first colorless and transparent, becomes larger and more granular; assuming a black, brown, yellow, or orange hue. In the mammalian vitellus the change consists only in an increase of size and granulation, without remarkable alteration of color.

As the eggs approach maturity, they gradually distend the Graafian follicles and project from the surface of the ovary. When fully ripe, they are discharged by rupture of the follicles, and, passing into the oviducts, are conveyed to the external generative orifice, and there expelled. In successive seasons, successive crops of eggs enlarge, ripen, leave the ovaries, and are discharged; and in many animals, the eggs of no less than three different crops may be distinguished in the ovary, namely: 1st, those which are mature and ready to be discharged; 2d, those which are to ripen in the following season; and 3d, those which are yet inactive and undeveloped. In most fish and reptiles, as well as in birds, the ripening and discharge of eggs takes place once a year. In different quadrupeds it occurs annually, semi-annually, bi-monthly, or even monthly; but in every instance it is periodical, returning at regular intervals.

Action of the Oviducts and other Generative Passages.—In the frog, after the ripening of the eggs and their discharge from the ovarian follicles, they receive an additional investment in the oviducts. On leaving the ovary, they consist only of the dark-colored granular vitellus, inclosed in its vitelline membrane. Their passage through the oviduct is effected by the peristaltic contraction of its walls, aided by the abdominal muscles. During this passage, an albuminous substance, secreted by the oviduct, is deposited round each egg in successive layers, forming a thick envelope (Fig. 161). When the eggs are discharged, it absorbs moisture from the water in which they are deposited, and swells into a transparent gelatinous mass, in which the eggs are imbedded. By its subsequent liquefaction and absorption, it supplies material, for the nourishment of the embryo.

Fig. 161.

Mature Frogs' Eggs.—*a.* While still in the ovary. *b.* After passing through the oviduct.

In scaly reptiles and in birds, the oviducts perform a more important function. In the common fowl, the ovary consists of follicles of various size, loosely united by connective tissue, and containing eggs in different stages of development (Fig. 162, *a*). As the egg which is approaching maturity enlarges, it distends its follicle, and projects from the general surface of the ovary; so that it hangs at last into the peritoneal cavity, retained only by the attenuated wall of the follicle, and a slender pedicle containing its blood-vessels. A rupture of the follicle then occurs at its most prominent part, and the egg is discharged from the lacerated opening.

As the egg leaves the ovary, it consists of a large, globular, orange-colored vitellus, or "yolk," inclosed in a thin and transparent vitelline membrane. Immediately beneath the vitelline membrane, on the surface of the vitellus, is a round white spot, consisting of a layer of minute granules, termed the "cicatricula," in which the germinative vesicle was previously imbedded. At this time the germinative vesicle has usually disappeared; but the cicatricula is still an important part of the vitellus, and marks the spot from which the embryo begins its development.

From the surface of the ovary, the yolk projects into the orifice of the oviduct; and when discharged from its follicle, it is embraced by the expanded upper extremity of this tube, and commences its downward passage. In the fowl, the muscular coat of the oviduct is highly developed, and its peristaltic contractions urge the egg from above downward, somewhat as the œsophagus or the intestine transports the food in a similar direction. While passing through the first five or six centimetres of the oviduct (*c*, *d*), where the mucous membrane is smooth and transparent, the yolk absorbs a certain quantity of fluid, becoming consequently softer and more flexible. It then passes into a second division of the canal, in which the mucous membrane is thicker and more glandular in texture, and arranged in longitudinal folds. This portion (*d*, *e*) extends over about 22 centimetres, or more than one-half the length of the oviduct. In its upper part, it secretes a viscid material, which consolidates into a gelatinous deposit around the yolk, thus forming a second envelope, outside the vitelline membrane.

The peristaltic movements of the oviduct are such as to give a rotary, as well as a progressive motion to the egg; and by this means the two extremities of the gelatinous envelope become twisted in opposite directions, forming rope-like extensions at the two poles of the egg. They are termed the "chalazæ," or suspensory cords, and the membrane with which they are connected is the "chalaziferous membrane."

Throughout the remainder of this part of the oviduct, an albuminous substance is deposited in successive layers round the yolk, inclosing the chalaziferous membrane and chalazæ. This substance, the so-called albumen, or "white of egg," is gelatinous in consistency, nearly transparent, and of a faint amber color. It is deposited in greater abundance in front of the egg than behind it, and thus forms a conical projection anteriorly, while behind, its outline is parallel with the spherical surface of the yolk. In this way, the egg acquires, when covered with its albumen, an ovoid form, of which one end is round, the other pointed; the pointed extremity being directed downward, as the egg descends through the oviduct.

Fig. 162.

Female Generative Organs of the Fowl.—*a*. Ovary. *b*. Graafian follicle, from which the egg has just been discharged. *c*. Yolk, entering upper extremity of oviduct. *d*, *e*. Second portion of oviduct, in which the chalaziferous membrane, chalazæ, and albumen are formed. *f*. Third portion, in which the fibrous shell membranes are produced. *g*. Fourth portion laid open, showing the egg completely formed, with its calcareous shell. *h*. Canal through which the egg is discharged.

In the third division of the oviduct (*f*), which is about nine centimetres in length, the longitudinal folds of the mucous membrane are narrower and more closely packed than in the preceding portion. Its secretion condenses into a fibrous covering, composed of three layers, closely embracing the surface of the albuminous mass, and forming a tough, flexible, semi-opaque envelope for the whole. These layers are known as the external, middle, and internal fibrous membranes.

Finally the egg passes into the fourth division of the oviduct (*g*), which is wider than the rest of the canal, but only a little over five centimetres in length. Its mucous membrane, which is covered with abundant leaf-like villosities, exudes a fluid rich in calcareous salts. The external fibrous layer is permeated by this secretion; and afterward, owing to the reabsorption of fluid, the calcareous matter is deposited in its network. The deposit goes on, growing thicker and more condensed, until the membrane is converted into a white, opaque, brittle, calcareous shell. The egg is then forced through a narrow portion of the oviduct (*h*), and, gradually dilating the passages by its conical extremity, is discharged from the external orifice.

Fig. 163.

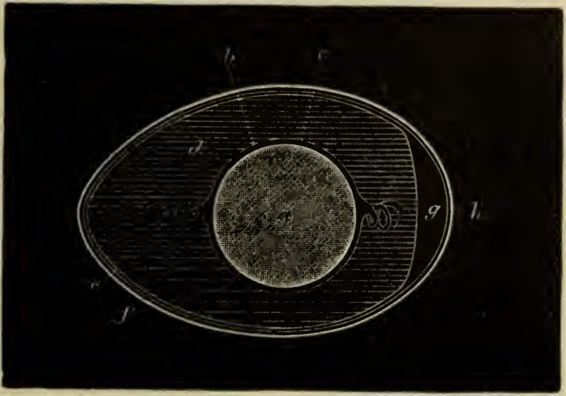


Diagram of Fowl's Egg.—*a*. Yolk. *l*. Vitelline membrane. *c*. Chalaziferous membrane. *d*. Albumen. *e*, *f*. Middle and internal shell membranes. *g*. Air-chamber. *h*. Calcareous shell.

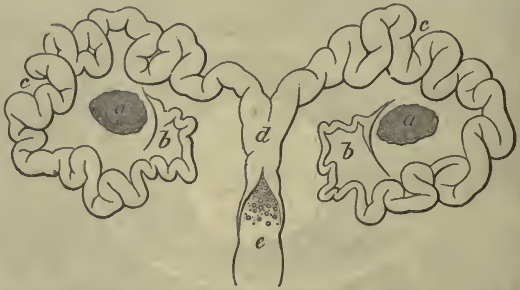
The egg of the fowl, after expulsion, consists, accordingly, of the yolk and vitelline membrane, with various additional parts acquired during its passage through the oviduct.

After the discharge of the egg there is a partial evaporation of its watery ingredients, which are replaced by air penetrating through the pores of the shell at its rounded extremity. The air thus introduced accumulates between the middle and internal fibrous membranes, forming a cavity or air-chamber (Fig. 163, *g*), at the rounded end of the egg. Very soon, the external layers of the albumen liquefy; and the vitellus, being specifically lighter, rises toward the surface of the egg, with the cicatricula uppermost. This part presents itself almost immediately on breaking open the egg at any point corresponding to the equator of the yolk, and is thus placed in the most favorable position for the action of warmth and air in the development of the chick.

In quadrupeds, the oviducts present a further modification. The egg, which is originally of minute size, is retained within the generative passages during the development of the embryo. While the upper part of the oviduct, accordingly, is narrow, and serves merely to transmit the egg from the ovary, and to supply it with a little albuminous secretion, the lower portions are much enlarged, and adapted for the protection and nourishment of the embryo. The upper and narrower portions of the oviduct are known as the "Fallopian tubes," from Fallopius* who first described them in the human female; while the lower and larger portions constitute the uterus. The two halves of the uterus unite with each other on the median line near their inferior termination, to form its "body;" while the ununited parts above are known as its "cornua" or horns.

In the human species, the ovaries consist of Graafian follicles, imbedded in a somewhat dense connective tissue, supplied with blood-vessels, and covered with an opaque, yellowish-white layer of fibrous tissue, called the "albugineous tunic." Its peritoneal layer is reflected in the usual way upon the blood-vessels supplying the organ, and is continuous with the broad ligaments of the uterus; but elsewhere it is closely consolidated with the albugineous tunic.

Fig. 164.



Uterus and Ovaries of the Sow.—*a, a.* Ovaries. *b, b.* Fallopian tubes. *c, c.* Horns of the uterus. *d.* Body of the uterus. *e.* Vagina.

The oviducts commence by a wide expansion, with fringed edges, called the "fimbriated extremity of the Fallopian tube." For most of their length they are narrow and convoluted, terminating, on each side, in the body of the uterus. This part of the organ is so much developed at the expense of the cornua, that the latter hardly appear to have an existence in the human species, and no trace of them is visible externally. But on opening the uterus, its cavity is seen to be somewhat triangular in shape, its upper corners running out to join the lower extremities of the Fallopian tubes. The cornua are therefore

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* Opera Omnia. Francofurti, 1600. Observationes Anatomicæ, p. 421.

consolidated with the body of the uterus, and enveloped in its thick layer of muscular fibres.

The mucous membrane of the body of the uterus in its usual condition is smooth, of a rosy color, and closely adherent to the subjacent muscular tissue. It consists of tubular follicles, ranged side by side, and opening on its free surface. Their secretion is probably destined for the nutrition of the embryo during the early periods of its formation.

The cavity of the body of the uterus terminates below by a constricted portion, termed the os internum, by which it is separated from the cervix. The inner surface of the cervix is raised in prominent ridges, arranged usually in two sets, diverging on each side from a central longitudinal ridge; presenting the appearance known as the "arbor vitæ uterina." The follicles of this part of the uterine mucous membrane are of a sac-like form, and secrete a tenacious mucus, which serves during gestation, to block up the cavity of the cervix, and thus prevent the escape or injury of the egg.

Fig. 165.

Generative Organs of the Human Female.—*a*, *a*. Ovaries. *b*, *b*. Fallopian tubes. *c*. Body of the uterus. *d*. Cervix. *e*. Vagina.

The cervix uteri presents inferiorly a second constriction, the "os externum;" and below this comes the vagina, constituting the last division of the female generative passages.

The accessory female organs of generation consist, therefore, of ducts, through which the egg is transported from within outward, varying in development, in different animals, according to the functions which they perform. In the lower orders, they serve mainly to convey the egg to the exterior, and to surround it more or less abundantly with albuminous secretions; while in the mammalia and in man, they are adapted to the more important office of retaining the egg during gestation and providing a vascular supply for the nourishment of the embryo.

CHAPTER III.

THE SPERMATIC FLUID, AND THE MALE ORGANS OF GENERATION.

THE mature egg is not by itself capable of being developed into an embryo. If simply discharged from the ovary and carried through the oviducts to the exterior, it dies and is decomposed, like any other part of the body separated from its connections. It is only when fecundated by the spermatic fluid, that it acquires the capacity for continued development.

The product of the male generative organs is a colorless, somewhat viscid, albuminous fluid, containing minute filamentous bodies, the *spermatozoa.* They have received this name on account of their active and continuous movement, suggesting the idea of independent animal organization.

Anatomical Characters of the Spermatozoa.—The spermatozoa of man (Fig. 166, *a*) are about .045 millimetre in length, according to the measurements of Kölliker. They present at one end a somewhat flattened, triangular-shaped enlargement, termed the "head," which constitutes about one-tenth part of their length. The remaining portion is a slender filamentous prolongation, called the "tail," which tapers gradually backward, becoming toward its extremity so attenuated that it is difficult to be seen except when in motion. There is no further organization visible in the spermatozoon; and it appears to consist, so far as can be seen by the microscope, of a homogeneous substance. The terms head and tail are not used, when describing the spermatozoon, in the same sense as that in which they would be applied to the corresponding parts of an animal; but simply for convenience, as one might speak of the head of an arrow or the tail of a comet.

In vertebrate animals, generally, the spermatozoa are similar in form to those of man; that is, they are filamentous bodies, with the anterior extremity more or less enlarged. In the rabbit, the head is roundish, and flattened, somewhat like a blood globule. In the rat (Fig. 166, b) it is conical, often slightly curved at its anterior extremity; and the whole spermatozoon is much longer than in man, measuring nearly 0.20 millimetre in length. In amphibia and reptiles generally, the spermatozoa are longer than in quadrupeds; and in Menobranchus, they are (Fig. 166, *c*), not less than 0.57 millimetre long, about one-third being occupied by the head or enlarged portion of the filament.

The most remarkable peculiarity of the spermatozoa, visible by the microscope, is their movement. In a drop of fresh spermatic fluid, sufficiently moistened and at its normal temperature, the numberless filaments with which it is crowded are seen to be in incessant motion. In many species of animals, the movement of the spermatozoa strongly resembles that of a tadpole; particularly in the mammalia, where they consist of a short, well-defined head, with a long and slender tail. The tail-like filament is in constant lateral vibration, by which the spermatozoon is driven from place to place in the surrounding fluid, as a fish or a tadpole is propelled through the water. In other instances, as in the Triton, or water-lizard, the spermatozoa have a writhing or spiral-like movement; presenting a peculiarly striking appearance when large numbers are viewed together.

Notwithstanding the energy and rapidity of this movement, and its resemblance in mechanism to animal locomotion, it has no analogy with a voluntary act.

Fig. 166.

Spermatozoa.—*a.* Human. *b.* Of the rat. *c.* Of Menobranchus. Magnified 480 times.

The spermatozoa are organic forms, produced in the testicles, and constituting at first a part of their tissue. Like the egg, the spermatozoon is destined to be discharged from the organ where it grew, retaining for a time its vital properties. One of these properties is its power of movement; but this does not indicate the possession of independent vitality, and is not even a proof of its animal origin. The movement of a spermatozoon is not more active than that of a bacterium cell, or of the ciliated zoospores of certain fresh-water algæ. It is analogous to the motion of a ciliated epithelium cell detached from its mucous membrane, which will sometimes continue for many hours, under favorable conditions of temperature and moisture. The movement of the spermatozoa continues for a time after their separation from the body; but it is limited in duration, and after a certain interval comes to an end.

In order to preserve their vitality, the spermatozoa must be kept at or near the normal temperature of the body, and protected from the contact of air or other unnatural fluids. If the spermatic fluid be allowed to dry, or if it be diluted with water, in the case of birds and quadrupeds, or if subjected to extremes of heat or cold, the motion of the spermatozoa ceases, and they soon disintegrate.

Formation of the Spermatozoa.—The testicles, within which the spermatozoa are produced, are the characteristic organs of the male sex, as the ovaries are characteristic of the female. In man and mammalia, they are solid, ovoid-shaped bodies, composed mainly of long, narrow, convoluted tubes, the "seminiferous tubes," lying for the most part closely in contact with each other, and separated only by capillary blood-vessels and a little connective tissue. The seminiferous tubes commence, by rounded extremities, near the external surface of the testicle and pursue an intricately convoluted course toward its central and posterior part. They are not strongly adherent to each other, and may be readily unravelled by manipulation.

According to Kölliker, the formation of the spermatozoa takes place within peculiar cells occupying the cavity of the seminiferous tubes. As puberty approaches, beside the ordinary pavement epithelium lining the tubes, larger cells make their appearance, each containing from one to twenty nuclei, with nucleoli. In these cells the spermatozoa are formed; their number corresponding usually with that of the cell-nuclei. They are developed in bundles, held together by the membranous envelope surrounding them, but are afterward set free by the liquefaction of the cell-wall, and mingled with a small quantity of transparent fluid.

While in the seminiferous tubes, the spermatozoa remain inclosed in their parent vesicles; they are liberated, and mingled together, only after entering the rete testis and the head of the epididymis.

Accessory Male Organs of Generation.—Beside the testicles, there are certain accessory organs by which the spermatic fluid is conveyed to the exterior, and mingled with various secretions which assist in the accomplishment of its function.

As the spermatozoa leave the testicle, they are crowded together in an opaque, white, semi-fluid mass, which fills the vasa efferentia, and distends their cavities. It then enters the single duct forming the body and lower extremity of the epididymis, following the tortuous course of this tube, until it reaches the vas deferens, by which it is conveyed to the vesiculæ seminales. Throughout this course it is mingled with a scanty mucus-like fluid, secreted by the epididymis and vas deferens. The vesiculæ seminales also contain a fluid secretion, which serves some secondary purpose in completing the formation of the sperm. One of its functions is no doubt to dilute the mass of spermatozoa, and give them liberty of motion; as well as to increase the volume of the spermatic fluid, and thus enable it to be expelled by the muscular contraction of the parts about the urethra. Kölliker has found the spermatozoa in the vas deferens and epididymis generally quiescent; their motion being exhibited only in the vesiculæ seminales and in the ejaculated sperm.

At the moment of its evacuation, the sperm first passes from the vesiculæ seminales into the prostatic portion of the urethra, where it meets with the secretion of the prostate gland, then poured out in unusual abundance; and farther on, there are added the secretions of Cowper's glands and of the remaining mucous follicles of the urethra. All these increase the volume of the spermatic fluid, and serve as vehicles for the transport of the spermatozoa.

Conditions of Fecundation by the Spermatic Fluid.—There are several conditions which are essential to the accomplishment of fecundation.

First, the spermatozoa must be present and in a state of vitality. Of all the organic ingredients, derived from different sources, which go to make up the spermatic fluid, the spermatozoa form the essential part. They are the fecundating element of the sperm, while the rest perform only accessory functions.

Spallanzani * found that if frog's sperm be passed through a succession of filters, so as to separate the solid from the liquid portions, the filtered fluid is destitute of fecundating properties; while the spermatozoa entangled in the filter, if mixed with a sufficient quantity of fluid, may be successfully used for the impregnation of eggs. The removal of both testicles destroys the power of impregnating the female, notwithstanding that all the other generative organs may remain uninjured. The spermatic fluid, furthermore, must be in a fresh condition, and the spermatozoa must retain their anatomical characters and their active movement. The experiments of Spallanzani have shown that, if the above conditions be preserved, the fluid, removed from the spermatic ducts of the male, is capable of fecundating the eggs of the female. But if exposed for a certain time to the atmosphere, or to unnatural temperatures, it becomes inert. So long as the spermatozoa continue in active motion, they are usually found to retain their physiological properties; the cessation of movement indicating that their vitality is exhausted, and that they are no longer capable of impregnating the egg.

Secondly, both eggs and spermatozoa must have arrived at a certain degree of development before fecundation can take place. Previous to this time the immature eggs are incapable of being impregnated, and the imperfectly developed spermatozoa have not yet acquired their fecundating power. The necessary growth takes place within the generative organs; and when it is complete, both spermatozoa and eggs are ready to be discharged, and are in condition to exert and receive the necessary influence.

The fecundating power of the spermatozoa is exceedingly active. Spallanzani found one-fifth of a gramme of the spermatic fluid of the frog, diffused in water, sufficient for the impregnation of several thousand eggs. The process seems to be accomplished almost instantaneously, "since eggs which were allowed to remain in the fecundating

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* Expériences pour servir à l'Histoire de la Génération. Genève, 1786.

mixture for only one second proved to be impregnated, and were afterward hatched at the usual period."

Thirdly, the spermatozoa must come in direct contact with the egg or its envelopes. Spallanzani first demonstrated this by attaching mature eggs to the concave surface of a watch-glass, which he placed, inverted, over a second watch-glass containing spermatic fluid. The eggs, exposed in this way for several hours to the vapor of the fluid without touching its surface, were afterward found to have failed of impregnation; while others, which had been moistened with the same spermatic fluid, became developed into tadpoles.

Finally, in the act of fecundation the spermatozoa penetrate, through the vitelline membrane, to the vitellus. This fact, first observed by Barry* in the rabbit, has subsequently been seen by Newport† in the frog, by Bischoff, by Coste, by Robin‡ in a species of leech, by Flint§ in the pond snail, and by Weil,‖ in repeated instances, in the rabbit. According to some of these observations, the penetration of the spermatozoon takes place by a small orifice or "micropyle" in the vitelline membrane, as first indicated by Barry. In others no such orifice has been visible; the spermatozoa appearing to perforate the vitelline membrane by the impulsive movement of their filamentous extremity (Newport). Such a mode of penetration is not inadmissible, since it is known that the much larger embryos of tænia and trichina make their way without difficulty through the substance of the intestinal mucous membrane.

After their arrival in the vitelline cavity, the spermatozoa disappear as distinct organic elements. Their substance unites with that of the vitellus; and thenceforward the fecundated egg is derived from both male and female organisms. The greater portion of its material is produced by the female; but that which is supplied from the seminal filaments of the male is equally essential for the production of an embryo. The offspring, accordingly, may exhibit resemblances to either or both of the parents, since it originates from both the generative products.

Union of the Sexes.—In most animals there is a periodical development of the testicles in the male, corresponding in time with that of the ovaries in the female. As the ovaries enlarge and the eggs ripen in one sex, the testicles of the other increase in size, and become turgid with spermatozoa. The accessory organs of generation at the same time exhibit an unusual activity of nutrition, increasing in vascularity and preparing to perform their part in reproduction.

In fishes, as a rule, the testicles occupy, in the abdomen of the male, the same relative position as the ovaries in the female; and, as they

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* Philosophical Transactions. London, 1840, p. 533, and 1843, p. 33.

† Ibid., 1853, p. 271.

‡ Journal de la Physiologie de l'Homme et des Animaux. Paris, 1862, tome v., p. 80.

§ Physiology of Man. New York, 1874, vol. v., p. 352.

‖ Stricker's Medicinischer Jahrbücher. Wien, 1873, p. 18.

become distended with their contents, they project into the peritoneal cavity. Each of the sexes is then under the influence of a corresponding excitement. The unusual development of the reproductive organs reacts upon the general system, producing a peculiar condition, known as "erethism." The female, distended with eggs, feels the stimulus which leads to their expulsion; while the male, bearing the weight of the enlarged testicles and the accumulation of newly-developed spermatozoa, is impelled by a similar sensation to the discharge of the spermatic fluid. The two sexes are led by instinct at this season to frequent the same situations. The female deposits her eggs in some spot favorable to their protection and development; after which the male, apparently attracted and stimulated by the sight of the new-laid eggs, discharges upon them the spermatic fluid, and thus effects their impregnation. It is in this way that fecundation takes place in nearly all the osseous fishes.

In instances like the above, where the male and female generative products are discharged separately, their subsequent contact would seem to be dependent on fortuitous circumstances, and impregnation, therefore, liable to fail. But, in fact, the simultaneous excitement of the sexes, leading them to ascend the same rivers and to frequent the same localities, provides with sufficient certainty for impregnation. The number of eggs produced by the female is also very large, the ovaries being often so distended as nearly to fill the abdominal cavity; so that, although many eggs may be accidentally lost, a sufficient number are still impregnated to provide for the continuation of the species.

In cartilaginous fishes, as in sharks, rays, and skates, an actual contact takes place between the sexes, and the spermatic fluid of the male is introduced into the female generative passages. Thus the eggs are fecundated within the body of the female, and in many species go through with a nearly complete development in this situation and the young are born alive.

In the frog, the male fastens himself on the back of the female by means of the anterior limbs, which retain their hold by spasmodic contraction. This continues for one or more days, during which time the mature eggs, after being discharged from the ovary, are passing through the oviducts. As they are expelled from the anus, the spermatic fluid is discharged upon them, and impregnation takes place.

In serpents, lizards, and turtles, the sperm is introduced into the female generative passage at the time of copulation, by means of an erectile male organ. Of these animals, some lay their eggs immediately after fecundation, others retain them until the embryo is partly developed.

In birds, the spermatozoa are introduced into the sexual orifice of the female, and make their way into the upper portion of the oviduct, where they may be found in active motion, mingled with the secreted fluids of this part of the canal.* The vitellus is thus fecundated immediately upon its discharge from the ovary, and before it has become surrounded with the albuminous envelopes supplied by the oviduct.

Lastly, in man and mammalians, where the impregnated egg is retained within the body of the female during the whole of its development, the spermatic fluid is introduced into the vagina and uterus by sexual congress, and meets the egg at or soon after its discharge from the ovary. A close correspondence between the periods of sexual excitement, in the male and the female, is visible in many of these animals, as well as in fish, birds, and reptiles. This is the case in most species which produce young but once a year, as the deer, the wolf, and the fox. In others, such as the dog, the rabbit, and the guinea-pig, where several broods of young are produced annually, or where, as in man, the generative epochs of the female recur at short intervals, the time of impregnation is comparatively indefinite, and the generative apparatus of the male is almost constantly in full development. It is excited to action at particular periods, apparently by some influence derived from the condition of the female.

In quadrupeds and in man, the contact of the sperm with the egg, and the fecundation of the latter, take place in the generative passages of the female; either in the uterus, the Fallopian tubes, or on the surface of the ovary—in each of which situations the spermatozoa have been found after sexual intercourse.

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* Foster and Balfour, Elements of Embryology. London, 1874, p. 21.

CHAPTER IV.

OVULATION AND MENSTRUATION.

Ovulation.

THE periodical ripening of the eggs and their discharge from the ovaries constitute the process of "ovulation," which may be considered as the primary act of reproduction. Its characteristic phenomena depend on the following general laws, which apply with but little variation to all classes of animals.

1. *Eggs exist originally in the ovaries, as part of their structure.* In fish, reptiles, and birds, the ovary is comparatively simple, consisting only of Graafian follicles, united by connective tissue, and thus aggregated into the form of a rounded, elongated, or lobulated organ. In the mammalians and in man, its essential constitution is the same; but its connective tissue is denser and more abundant, and its texture more compact. In all classes each Graafian follicle contains an egg, which varies in size in different species and at different periods of growth.

The process of reproduction is not essentially different in oviparous and viviparous animals. In the oviparous classes, including most fishes and reptiles and all birds, the female produces an egg, of considerable size, from which the young is afterward hatched; while in those which are viviparous the young is brought forth, already formed and alive, from the body of the female. But examination shows that the ovaries of viviparous animals also contain eggs, analogous to those of the ovipara, though of smaller size and comparatively simple structure.

The distinction between the two classes, so far as regards the process of reproduction, is therefore apparent rather than fundamental. In the oviparous fish, reptiles, and birds, the egg is discharged before or immediately after impregnation, the embryo being developed and hatched externally. In quadrupeds and in man, on the other hand, the egg is retained within the body of the female until the formation of the embryo is complete; when the membranes are ruptured and the young expelled. But in all instances, the young is produced from an egg; and the egg, though presenting variations of size and structure, always consists essentially of a vitellus and a vitelline membrane, and is first formed in the interior of an ovarian follicle.

The egg is accordingly a part of the ovarian tissue. It exists before the generative function is established, and during the earliest periods of life. It is found without difficulty in the newly-born female infant, and may even be detected in the fœtus before birth. Its nutrition is provided for in the same manner with that of other parts of the bodily structure.

2. *The ovarian eggs become more fully developed at a certain age when the generative function is about to be established.* During the early periods of life, the ovaries and their contents, like many other organs, are imperfectly developed. They exist, but they are as yet incapable of functional activity. In the young chick, the ovary is small; and the eggs, instead of presenting a voluminous, yellow, opaque vitellus, are minute, transparent, and colorless. In young quadrupeds, and in the human female during infancy and childhood, the ovaries are equally quiescent. They are small, friable, and of nearly homogeneous appearance to the naked eye; presenting none of the enlarged follicles, filled with transparent fluid, which afterward become a characteristic feature of their structure. At this time, accordingly, the ovaries are inactive, the eggs which they contain immature, and the female incapable of bearing young.

But at a certain period, which varies in the time of its occurrence in different species, the sexual apparatus enters upon a state of activity. The ovaries increase in size, and their eggs, which have previously remained quiescent, take on a rapid growth, the structure of the vitellus being completed by a deposit of semi-opaque granular matter in its substance. In this condition, the eggs are ready for impregnation, and the female becomes capable of bearing young. She is then said to have arrived at the state of "puberty," in which the generative organs are fully developed. This change is accompanied by a corresponding alteration in the system at large. In many birds, the plumage assumes more varied and brilliant colors; and in the common fowl, the comb, or "crest," enlarges and becomes red and vascular. In the American deer (Cervus virginianus), the coat, which during the first year is mottled with white, changes in the second year to a reddish tinge. In nearly all species, the limbs become more compact and the body more rounded; and the whole external appearance is so altered as to indicate that the animal has arrived at the period of puberty, and is capable of reproduction.

3. *In the adult female, successive crops of eggs ripen and are discharged by rupture of the Graafian follicles.* The eggs are not only formed and attain their growth within the ovaries, but they are also ripened and discharged, irrespective of sexual intercourse, from the independent functional activity of the female organism. In many fishes and reptiles, the mature eggs leave the ovary, pass through the oviducts, and are discharged before coming in contact with the spermatic fluid of the male. The domestic fowl, if well supplied with nourishment, will continue to lay eggs without the presence of the cock; only these eggs, not having been fecundated, cannot produce chicks. In oviparous animals, therefore, the discharge of the egg, as well as its formation, may take place independently of sexual intercourse.

This is also true of the vivipara. The observations of Bischoff, Pouchet, and Coste, on the sheep, the pig, the bitch, and the rabbit, have demonstrated that if the female be kept from the male until after puberty, and then killed, examination of the ovaries will sometimes show that Graafian follicles have matured, ruptured, and discharged their eggs, though no sexual intercourse has taken place. Sometimes the follicles are found distended and prominent on the surface of the ovary; sometimes recently ruptured and collapsed; or in various stages of cicatrization and atrophy. Bischoff,* in several instances of this kind, found the unimpregnated eggs in the oviduct, on their way toward the uterus. In species where the ripening of the eggs takes place at short intervals, as in the sheep, the pig, or the cow, it is very rare to examine the ovaries without finding traces of a more or less recent rupture of Graafian follicles.

One of the most important facts, derived from these observations, is that the ovarian eggs become developed and are discharged in successive crops, and at regular intervals. In the ovary of the fowl (Fig. 162), it may be seen at a glance that the eggs grow and ripen, one after the other, like fruit upon a vine. In this instance, the process of evolution is rapid; and it is easy to distinguish, at the same time, eggs which are almost microscopic in size, colorless, and transparent; those which are larger, somewhat opaline, and yellowish; and finally those which are fully developed, of a deep, opaque orange hue, and nearly ready to leave the ovary.

The difference between the undeveloped and mature eggs, in the fowl's ovary, consists mainly in the size of the vitellus; and the ovarian follicle is distended and ruptured, and the egg finally set free, owing to the pressure of the enlarged vitellus.

In man and mammalians, on the other hand, the microscopic egg never becomes large enough to distend the Graafian follicle by its own size. The rupture of the follicle and the liberation of the egg are provided for, in these instances, by the following mechanism.

In the earlier periods of life, in man and mammalians, the egg is contained in a Graafian follicle which closely embraces its exterior, being hardly larger than the egg itself. As puberty approaches, the follicles situated near the surface of the ovary become enlarged by the accumulation of serous fluid in their cavity. At that time, the ovary contains a number of transparent vesicles, the smallest of which are deep seated, and which increase in size as they approach the free surface of the organ. These are the Graafian follicles, which gradually enlarge in consequence of the advancing maturity of their eggs.

The Graafian follicle then consists of a closed sac, the external wall of which, though translucent, has a fibrous texture, and is well supplied with blood-vessels. This fibrous and vascular wall is distinguished by the name of the "vesicular membrane." It is not very firm in texture, and if roughly handled is easily ruptured.

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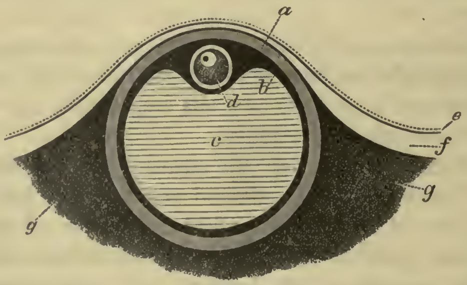
* Annales des Sciences Naturelles, Paris, Août—Septembre, 1844.

The vesicular membrane is lined throughout by a layer of granular cells, which form for it a kind of epithelium. This layer is termed the *membrana granulosa.* It adheres but slightly to the vesicular membrane, and may easily be detached by manipulation before the follicle is opened, when it appears mingled, in the form of light flakes and shreds, with the serous fluid of the follicle.

At the most superficial part of the Graafian follicle the membrana granulosa is thicker than elsewhere. Its cells are here accumulated, in a kind of mound or "heap," which has received the name of the *cumulus proligerus.* It is also called the *discus proligerus*, because the thickened mass, when viewed from above, has a circular or disk-like form. In the centre of the discus proligerus the egg is imbedded. It is accordingly always situated at the most superficial portion of the follicle, nearest the surface of the ovary.

As the period approaches for the discharge of the egg, the Graafian follicle becomes more vascular, and enlarges by an increased exudation into its cavity. It then begins to project from the surface of the ovary, still covered by the albugineous tunic and its peritoneal investment. (Fig. 167.) The accumulation of fluid exerts such a pressure from within, that the albugineous tunic and peritoneum gradually yield before it; until the Graafian follicle protrudes from the ovary as a tense, rounded, translucent vesicle, in which fluctuation can be perceived on applying the fingers to its surface. Finally, the process of effusion and distention still going on, the wall of the follicle gives way at its most prominent portion, and the contained fluid is expelled by the elastic reaction of the ovarian tissue, carrying with it the egg, entangled in a portion of the membrana granulosa.

FIG. 167.



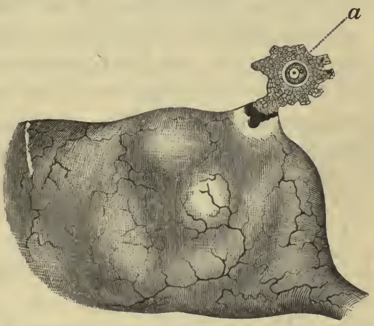
GRAAFIAN FOLLICLE, near the period of rupture.—*a.* Vesicular membrane. *b.* Membrana granulosa. *c.* Cavity of follicle. *d.* Egg. *e.* Peritoneal surface. *f.* Tunica albuginea. *g, g.* Tissue of the ovary.

The rupture of the Graafian follicle is accompanied, in some instances, by hemorrhage from its inner surface, by which it is filled with blood. This occurs in the human species, in the pig, and to some extent in several other animals. Sometimes, as in the cow, where there is no immediate hemorrhage, the Graafian follicle collapses at the time of rupture; after which a slight exudation, more or less tinged with blood, is poured out in the course of a few hours.

This process occurs in one or more follicles at a time, according to the number of young to be produced. In the bitch and the sow, where each litter consists of from five to twenty young, a similar number of eggs ripen and are discharged at each period. In the mare, the cow, and the human female, where there is usually but one fœtus at a birth, the eggs are matured singly, and the Graafian follicles ruptured, one by one, at successive periods of ovulation.

4. *The ripening and discharge of the egg are accompanied by a peculiar condition of the general system, known as "rutting," or "œstruation."* The congestion and functional activity shown by the ovaries, at each period of ovulation, extend to the other generative organs, producing in them more or less excitement, according to the species of animal. Usually there is vascular congestion of the entire generative apparatus. The secretions of the vagina and neighboring parts are increased in quantity and altered in quality. In the bitch, the vaginal mucous membrane becomes red and tumefied, and pours out a secretion more or less tinged with blood, and possessing a peculiar odor, which appears to attract the male. An unusual tumefaction and redness of the vagina and vulva are also perceptible in the rabbit; and in some apes there is not only a bloody discharge from the vulva, but engorgement and infiltration of the neighboring parts, extending to the buttocks, the thighs, and the under part of the tail.*

FIG. 168.



OVARY WITH GRAAFIAN FOLLICLE RUPTURED: at *a*, the egg, just discharged, with a portion of the membrana granulosa.

The system at large is also affected. In the cow, the approach of an œstrual period is marked by unusual restlessness. The animal partially loses her appetite. She frequently stops browsing, looks about uneasily, runs from one side of the field to the other, and then recommences feeding, to be again disturbed in a similar manner after a short interval. The motions are rapid and nervous, and the hide rough and disordered, indicating the presence of some special excitement. After œstruation is fully established, the vaginal secretions continue for one or two days unusually abundant; after which the symptoms subside, and the animal returns to her usual condition.

In these animals the female will allow the approach of the male only during or immediately after the œstrual period; that is, when the egg is recently discharged, and ready for impregnation. At other times,

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* Pouchet, Théorie positive de l'ovulation. Paris, 1847, p. 230.

when sexual intercourse would be fruitless, the instinct of the animal leads her to avoid it; and the concourse of the sexes accordingly corresponds in time with the maturity of the egg and its aptitude for fecundation.

Menstruation.

In the human female, the periodical excitement of the generative apparatus is marked by a group of phenomena known as *menstruation*, which are of sufficient importance to be described by themselves.

During infancy and childhood the sexual system is inactive. No eggs are discharged from the ovaries, and no external phenomena show themselves, connected with the reproductive function.

But at the age of fourteen or fifteen years, a change becomes visible. The outlines of the body grow more rounded, the breasts increase in size, and the entire aspect undergoes a peculiar alteration, dependant on the approach of maturity. At the same time a discharge of blood takes place from the generative passages, accompanied by some disturbance of the general system, and the female is then known to have arrived at the period of puberty.

Afterward, the discharges recur at intervals of four weeks; and, from their correspondence in time with successive lunar months, they are designated as the "menses" or "menstrual periods." These periods are usually regular in recurrence, from their first appearance, until about the age of forty-five years. During this time the female is capable of bearing children, and sexual intercourse is liable to be followed by pregnancy. After the forty-fifth year, the periods first become irregular, and then cease; their final disappearance being an indication that pregnancy cannot again take place.

Between the ages of fifteen and forty-five years, the regularity of the menstrual periods indicates to a great extent the individual aptitude for impregnation. All causes of ill health which derange menstruation are also apt to interfere with pregnancy; and women whose menses are regular are more likely to become pregnant, after sexual intercourse, than those in whom the periods are absent or irregular.

When pregnancy takes place, however, the menses are suspended during its continuance. They usually remain absent, after delivery, until the end of lactation, when they recommence, and recur at regular intervals, as before.

When the menstrual period is about to come on, the female is usually affected with some degree of discomfort and lassitude, a sense of weight in the pelvis, and a more or less disinclination to society. These symptoms are in some instances slightly pronounced, in others more distinct. A discharge of vaginal mucus then begins to take place, soon becoming yellowish or rusty-brown in color, from the admixture of blood; and by the second or third day it has the appearance of nearly pure blood. The unpleasant sensations, at first manifest, then usually subside; and the discharge, after continuing for two or three days longer, grows more scanty. Its red color diminishes in intensity, becoming brownish or rusty, until it finally disappears, and the process comes to an end.

The menstrual periods of the human female correspond with those of œstruation in animals. Like them, they are absent in the immature condition, and begin only at the time of puberty, when the aptitude for impregnation commences. Like them, they recur during the child-bearing period at regular intervals, and are liable to the same interruption by pregnancy. Finally, their disappearance corresponds with the cessation of fertility.

The periods of œstruation, in many animals, are accompanied with an unusual discharge from the generative passages, frequently more or less tinged with blood. In the human female the bloody discharge, though more abundant, differs only in degree from that which exists in other instances.

But the most complete evidence that the menstrual periods coincide with ovulation, is derived from direct observation. A sufficient number of instances have been recorded to show that at the time of menstruation a Graafian follicle becomes enlarged, ruptures, and discharges its egg. Cruikshank* noticed such a case in 1797. Négrier† relates two instances in which, after sudden death during menstruation, a bloody and ruptured Graafian follicle was found in the ovary. Bischoff‡ speaks of four similar cases, in three of which the follicle was just ruptured, and in the fourth distended, prominent, and ready to burst. Coste§ met with several of the same kind. Michel‖ found a follicle ruptured and filled with blood in a woman who was executed for murder while the menses were present. Two instances are reported by Letheby,¶ in one of which he succeeded in finding the ovum in the corresponding Fallopian tube. We have also met with two instances of Graafian follicles freshly ruptured and filled with blood, in women who died during or immediately after menstruation.

Ovulation, accordingly, in the human female, accompanies and forms a part of menstruation. As the menstrual period comes on, a congestion takes place throughout the generative apparatus; in the Fallopian tubes and the uterus, as well as in the ovaries and their contents. One of the Graafian follicles is especially the seat of vascular excitement. It becomes distended by the accumulation of fluid in its cavity, projects from the surface of the ovary, and is finally ruptured; the process taking place essentially as in mammalian animals.

It is not certain at what precise time during the menstrual flow the rupture of the follicle takes place. According to Bischoff, Pouchet, and Raciborski, it usually happens, not at the commencement, but toward

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* Philosophical Transactions. London, 1797, p. 135.

† Recherches sur les Ovaires. Paris, 1840, p. 78.

‡ Annales des Sciences Naturelles. Paris, Août, 1844.

§ Histoire du Développment des Corps Organisés. Paris, 1847, tome i., p. 221.

‖ American Journal of the Medical Sciences. Philadelphia, July, 1848.

¶ Philosophical Transactions. London, 1852, p. 57.

the termination of the period. According to Coste,* it is sometimes earlier, sometimes later. So far as we can determine, its precise period is not invariable. Like the menses themselves, it may be hastened or retarded according to circumstances; but it always occurs in connection with the menstrual flow, and constitutes the most important part of the process in regard to reproduction.

The egg, when discharged from the ovary, enters the fimbriated extremity of the Fallopian tube, and commences its passage toward the uterus. The mechanism by which it finds its way into and through the Fallopian tube in quadrupeds and man is different from that in birds and reptiles. In the latter, the bulk of the eggs is sufficient to distend the oviduct; and the mass, embraced by the muscular wall of the canal, is carried downward by peristaltic action. In mammalians, on the other hand, the egg is microscopic in size. The wide extremity of the Fallopian tube, directed toward the ovary, is lined with ciliated epithelium; and the movement of the cilia, which is from the ovary toward the uterus, produces a kind of vortex, by which the egg is conducted into the narrow portion of the tube, and thence downward to the uterus.

Accidental causes may sometimes disturb the passage of the egg. It may be arrested at the surface of the ovary, and thus fail to enter the Fallopian tube. If it be fecundated and go on to partial development in this situation, it gives rise to "ovarian pregnancy." It may escape from the fimbriated extremity of the Fallopian tube into the peritoneal cavity, and form attachments to a neighboring organ, causing "abdominal pregnancy;" or finally it may stop in some part of the Fallopian tube, and thus give origin to "tubal pregnancy."

The egg, immediately after its discharge from the ovary, is ready for impregnation. If sexual intercourse take place about that time, the egg and the spermatozoa meet in some part of the female generative passages, and fecundation is accomplished. It appears from the observations of Bischoff, Coste, and Barry† upon rabbits, that the contact of the egg and the spermatozoa may take place either in the uterus or the Fallopian tubes, or on the surface of the ovary. If, on the other hand, there be no sexual coitus, the egg passes the Fallopian tube unimpregnated, loses its vitality after a time, and is carried away with the uterine secretions.

For this reason sexual intercourse is most liable to be followed by pregnancy when occurring at or soon after the menstrual epoch. Before its discharge, the egg is immature and unfit for impregnation; and some days afterward, it loses its freshness and vitality. The exact length of time, preceding and following the menses, during which impregnation is possible, has not been ascertained. The spermatozoa, on the one hand, retain their vitality for an unknown period after coition, and the egg for an unknown period after its discharge. These

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* Histoire du Développment des Corps Organisés. Paris, 1847, tome i., p. 221.

† Philosophical Transactions. London, 1839, p. 315.

occurrences may either precede or follow each other within certain limits, and impregnation may still take place; but the precise extent of these limits is undetermined, and is probably more or less variable in different individuals.

Lastly, there are exceptional cases in which fertility exists without a menstrual flow, and menstruation without ovulation. If we regard the rupture of an ovarian follicle and hemorrhage from the uterus, in menstruation, as two phenomena normally coincident, excited by a common cause, and subservient to the same general function, we must still recognize the possibility of either one being deranged independently of the other. Various authors (Churchill, Reid, Velpeau) have related instances of fruitful women in whom the menses were scanty and irregular, or even absent. The menstrual flow is habitually scanty in some individuals, and abundant in others. Such variations depend on the vascular activity of the system at large, or of the uterine organs in particular; and though the bloody discharge is usually an index of the aptitude of these organs for impregnation, it is not invariably so. Provided a mature egg be discharged from the ovary, pregnancy is possible although the menstrual flow be absent.

On the other hand we have met with a fully authenticated instance* in which menstruation recurred regularly for several months without the rupture of a Graafian follicle; and twelve cases have been collected by Goodman † in which menstruation continued notwithstanding the removal of both ovaries, in the adult, by ovariotomy. But where the ovaries are congenitally undeveloped, menstruation is also absent, and the sexual system inactive.

The blood which escapes during the menstrual flow is supplied by the uterine mucous membrane. After death during menstruation, the internal surface of the uterus is found smeared with a sanguineous fluid, which may be traced through the uterine cervix into the vagina. The Fallopian tubes are sometimes congested, and filled with a similar bloody discharge. The menstrual blood has also been seen to exude from the uterine orifice in cases of procidentia uteri, as well as in the normal condition by examination with the speculum. It is discharged by a kind of capillary hemorrhage, and, as a rule, does not form a visible coagulum, owing to its being exuded from many minute points, and mingled with mucus. When poured out more rapidly and abundantly, as in menorrhagia, it coagulates in the same manner as blood from other sources. Its discharge is, at the same time, the consequence and the natural termination of the uterine congestion.

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* Transactions of the American Gynæcological Society. Boston, 1878, vol. ii., p. 136.

† Richmond and Louisville Medical Journal, December, 1875.

CHAPTER V.

THE CORPUS LUTEUM, AND ITS CONNECTION WITH MENSTRUATION AND PREGNANCY.

AFTER the rupture of a Graafian follicle at the menstrual period, there is left in the ovary a bloody cavity, which is subsequently obliterated by a process somewhat similar to the healing of an abscess. The office of the Graafian follicle is to provide for the formation and growth of the egg in the ovary. After the discharge of the egg, the follicle has no further function to perform; and it then passes through a process of obliteration, as an organ which has become obsolete. While undergoing this change, it is at one time converted into a solid, spheroidal body, called the *corpus luteum;* a name derived from the yellow color acquired during its formation.

In quadrupeds, the corpus luteum is characterized by peculiarities of size, color, growth, and disappearance, which are distinctive for each species; although the general course of its formation and atrophy is the same in all. In the human female it is marked by a moderately large size, a brilliant yellow hue at certain periods of its development, and the presence of blood in its central cavity, distinguishable for two or three weeks after the rupture of the follicle. The details of its growth and retrocession, which follow a regular course during the normal recurrence of the menstrual periods, are modified by the existence of pregnancy. In the first instance, it is known as the *corpus luteum of menstruation;* in the second as the *corpus luteum of pregnancy.*

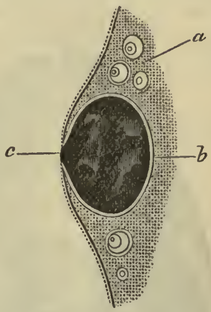
Corpus Luteum of Menstruation.

In the human female, during menstruation, at or immediately after the discharge of the egg, a somewhat abundant hemorrhage takes place from the inner surface of the Graafian follicle, by which its cavity is filled with blood. The blood soon coagulates, as it would if extravasated elsewhere, and the coagulum remains enclosed by the walls of the follicle. The opening by which the egg has escaped is usually a rounded perforation, not more than one millimetre in diameter; and a slender probe, introduced through this opening, passes directly into the cavity of the follicle. If the follicle be opened at this time by a longitudinal incision through the ovary (Fig. 169), it will be seen to form a spheroidal cavity, between one and two centimetres in diameter, containing the soft, recent, dark colored coagulum. The coagulum has no organic connection with the walls of the follicle, but lies loose in its cavity, and may be easily turned out with the handle of a scalpel. It has sometimes a slight mechanical adhesion to the edges of the lacerated opening; but there is no continuity of substance between them, and the clot may be everywhere separated by careful manipulation. The membrane of the vesicle presents a smooth, transparent, and vascular internal surface.

Soon afterward an important change takes place, both in the central coagulum and in the vesicular membrane.

The clot, which is at first large, soft, and gelatinous, begins to contract; and the serum separates from the coagulum proper. The serum is absorbed by the neighboring parts; and the clot, accordingly, grows smaller and denser. At the same time its coloring matter undergoes the usual changes which follow extravasation, and is partially reabsorbed together with the serum. This second change is somewhat less rapid than the former, but a diminution of color is usually perceptible in the clot, at the expiration of two weeks from the rupture of the follicle.

FIG. 169.



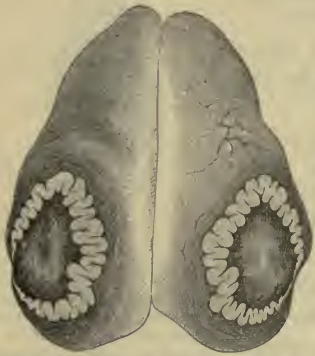
GRAAFIAN FOLLICLE of the human ovary; recently ruptured during menstruation, and filled with coagulated blood; longitudinal section.—*a*. Tissue of the ovary, containing unruptured Graafian follicles. *b*. Vesicular membrane of the ruptured follicle. *c*. Point of rupture.

The vesicular membrane at the same time takes on an increased development, by which it becomes thickened and convoluted, and tends partially to fill the cavity of the follicle. Its hypertrophy and convolution commences earliest and proceeds most rapidly at the deeper part of the follicle. From this point it becomes thinner and less convoluted toward the surface of the ovary and the edges of the ruptured orifice.

At the end of three weeks, the hypertrophy of the vesicular membrane has reached its maximum. The follicle has now become so altered by the growth above described, and by the condensation of its clot, that it presents the appearance of a solid body of new formation, and receives the name of "corpus luteum," although its yellow color is not yet distinctly developed. It causes a perceptible prominence on the surface of the ovary, and may be felt as a rounded tumor, in the ovarian tissue, nearly always somewhat flattened from side to side. It measures about 19 millimetres in length and about 12 millimetres in depth. On its surface there is a minute cicatrix, the mark of the original rupture.

On cutting it open at this time (Fig. 170), the corpus luteum is seen to consist, as above described, of a central coagulum and a convoluted wall. The coagulum is semi-transparent, of a gray or light-greenish color, more or less mottled with red. The convoluted wall is about three millimetres thick at its deepest part, and of an indefinite yellowish or rosy hue, not very different in tinge from the rest of the ovarian tissue. The convoluted wall and the contained clot lie in contact with each other, without intervening organic connection; and they may still be readily separated by the handle of a scalpel or the flattened end of a probe. The whole corpus luteum may also be stripped out, or enucleated from the ovarian tissue; and when extracted in this way, it presents itself as a spheroidal or flattened mass, with a convoluted external surface covered with remains of the connective tissue by which it was attached to the substance of the ovary.

FIG. 170.



HUMAN OVARY cut open, showing a corpus luteum, divided longitudinally; three weeks after menstruation. From a girl, twenty years of age, dead of hæmoptysis.

We have had an opportunity of examining a corpus luteum of this period, in an ovary immediately after its removal from the body of the living woman. It was on the occasion of the extirpation by Prof. T. T. Sabine, in 1874, of the left ovary for obstinate ovarian neuralgia, from an unmarried woman, otherwise healthy, 25 years of age.* The last menstrual period had terminated exactly three weeks before the date of the operation, and a new one commenced twenty-four hours afterward. The extirpated ovary presented a perfectly normal appearance, and contained a corpus luteum similar in all respects to that represented in Fig. 170. Its convoluted wall was fully formed, without any distinctly marked yellow tinge, and the central coagulum was partly, but not entirely, decolorized. The patient recovered without difficulty.

FIG. 171.

HUMAN OVARY, showing a corpus luteum, four weeks after menstruation; from a woman dead of apoplexy.

After the third week from the close of menstruation, the corpus luteum passes into a retrograde condition. It diminishes perceptibly in size, and the central coagulum continues to be absorbed and loses still farther its coloring matter. The whole body undergoes a process of atrophy; and at the end of the fourth week it is less than 10 millimetres in its longest diameter (Fig. 171). The external cicatrix may still be seen, as well as the point where the central coagulum lies in contact with the peritoneal surface. There is still no organic connection between the coagulum and the convoluted wall; but the condensation of the clot and the closer folding of the wall prevent the separation of the two being so easily accomplished as before. The entire corpus luteum may still be extracted from its bed in the ovarian tissue.

The color of the convoluted wall, during this stage, instead of fading,

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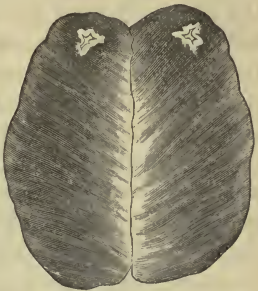
* New York Medical Journal, January, 1875, p. 37.

like that of the fibrinous coagulum, increases in intensity. From an indefinite yellowish or rosy hue, it gradually becomes a decided yellow. This change is produced simultaneously with a kind of fatty degeneration of its tissue; which presents at this time, under the microscope, a considerable deposit of oil globules. At the end of the fourth week, the alteration in hue is complete; and the outer wall of the corpus luteum is then of a clear chrome-yellow color, by which it is readily distinguishable from the neighboring parts.

After this period, degeneration goes on rapidly. The clot becomes dense and shrivelled, and is converted into a minute, stellate, white, or reddish-white cicatrix. The yellow wall grows softer and more friable, and exhibits less distinctly the marking of its convolutions. At the same time its surface becomes confounded with the central coagulum on the one hand, and with the neighboring parts on the other, so that it is no longer possible to separate them fairly from each other. At the end of eight or nine weeks (Fig. 172) the whole is reduced to an insignificant, yellowish, cicatrix-like spot, measuring about six millimetres in its longest diameter, in which the original texture of the corpus luteum can be recognized only by the peculiar folding and coloring of its constituent parts. Afterward its atrophy goes on more slowly, and seven or eight months may sometimes elapse before its complete disappearance.

FIG. 172.



HUMAN OVARY, showing a corpus luteum, nine weeks after menstruation; from a girl dead of tubercular meningitis.

The size of the corpus luteum depends on the quantity of blood exuded into the follicle at the time of its rupture, and on the more or less active growth of its convoluted wall. Both these conditions may no doubt vary in different cases, according to the general bodily development, and the size and vascularity of the ovaries in particular. In healthy women the weight of the ovaries, which is, on the average, five grammes each, varies frequently twenty per cent. above or below this standard; and even in the same individual the right and left ovaries are seldom of the same size; usually differing from each other by at least ten per cent. It is therefore impossible to fix an invariable standard of size for the corpus luteum, corresponding with its period of development. But it nevertheless follows, during the greater part of the intermenstrual period, a general course of enlargement, succeeded by a process of atrophy. The following list gives its weight as actually observed* in eight cases in which the date of menstruation was known.

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* Transactions of the American Gynecological Society. Boston, 1878, vol. ii., p. 130.

Weight of the Corpus Luteum.

	Milligrammes.
1. Two days after menstruation	380
2. Nine days after "	430
3. Ten days after "	810
4. Fifteen to twenty days after menstruation	1230
5. Twenty days after menstruation	1200
6. Six weeks after "	90
7. Ten weeks after "	20
8. Eleven weeks after "	15

The corpus luteum, accordingly, is a formation which results from the obliteration of a ruptured Graafian follicle. It is produced during the intermenstrual period, and occupies the substance of the ovary, immediately beneath the superficial cicatrix which marks the site of the rupture. After acquiring its maximum size about the end of the third week it passes into the retrograde condition and soon becomes obsolete; while a new body, of similar structure, is produced from the rupture of another Graafian follicle. In an ordinary intermenstrual period, therefore, the ovaries contain, as a rule, one corpus luteum of preponderating size, and in addition several which are more or less obsolete. Four, five, six, and even eight corpora lutea may thus be found in the ovaries at the same time, perfectly distinguishable by their texture, though very small, and for the most part in a state of advanced retrogression. As they finally disappear, one after the other, their number no longer corresponds with that of the Graafian follicles which have been ruptured.

Corpus Luteum of Pregnancy.

Since the process above described occurs at each menstrual period, the presence of a corpus luteum is no indication that pregnancy has existed, but only that a Graafian follicle has been ruptured and its contents discharged. Nevertheless, when pregnancy takes place, the history of the corpus luteum is different in some respects from that which follows an ordinary menstruation.

The distinction between the two kinds of corpora lutea is not an essential or fundamental difference; since they both originate in the same way, and are composed of the same structures. It depends on the difference in rapidity and degree of their development. While the corpus luteum of menstruation passes rapidly through its stages, and is soon reduced to a condition of atrophy, that of pregnancy continues its development for a longer time, attains a larger size and firmer organization, and disappears at a later period.

The variation of the corpus luteum in pregnancy is caused, no doubt, by the condition of the uterus. This organ exerts a wide influence, in the state of gestation, on many parts of the system. The stomach becomes irritable, the appetite is capricious, and even the mental and moral qualities are more or less affected. The ovaries feel this influence to such a degree that ovulation is arrested, and no more Graafian follicles are ruptured, during the whole term of pregnancy. It is not surprising that the growth of the corpus luteum should be modified from the same cause.

For the first three weeks of its formation the corpus luteum presents the same features in the impregnated as in the unimpregnated condition. But after that time a difference becomes manifest. Instead of commencing a retrograde course during the fourth week, it continues its development. The external wall grows thicker and more convoluted. Its color changes, as previously described, to a bright yellow; and it contains a deposit of fatty matter in the form of microscopic globules.

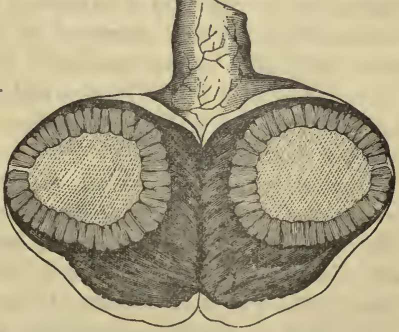
By the end of the second month of pregnancy, the corpus luteum has increased to 22 millimetres in length by 12 or 13 millimetres in depth. The central coagulum has become nearly decolorized, and presents the appearance of a fibrinous deposit. Sometimes a part of the serum, as it separates from the clot, accumulates in the centre of the mass, as in Fig. 173, forming a little cavity filled with clear fluid and inclosed by a fibrinous layer, the remains of the solid portion of the clot. The existence of such a cavity, however, is only occasional. More frequently, the fibrinous clot is solid throughout, all the serum being absorbed by the surrounding parts.

Fig. 173.

Corpus Luteum of pregnancy, at the end of the second month; from a woman dead from induced abortion.

During the third and fourth months, the enlargement of the corpus luteum continues; and at the end of that time it may measure 22 millimetres in length by 18 or 19 millimetres in depth. Its flattened form is very manifest, so that, in a longitudinal section, it may present a nearly circular outline, as in Fig. 174, while in a transverse section its figure is a narrow oval. The convoluted wall is still more highly developed than before, having a thickness, at its deepest part, of nearly 5 millimetres. Its color, however, has already begun to fade, assuming a dull yellowish tinge. The central coagulum, perfectly colorless and fibrinous, is often so much flattened laterally that it is hardly 2 millimetres in thickness.

Fig. 174.



Corpus Luteum of pregnancy, at the end of the fourth month; from a woman dead by poison.

The other relations between different parts of the structure remain the same.

The corpus luteum has now attained its maximum of development, and continues without very perceptible alteration during the fifth and sixth months. It then begins to retrograde, diminishing in size during the seventh and eighth months. Its external wall becomes still more faded, changing to a faint yellowish-white color, not unlike that presented at the end of the third week. It is thick, soft, and elastic, and numerous slender blood-vessels can be seen penetrating from without into the interstices of its convolutions. Its central coagulum is reduced to the condition of a whitish radiated cicatrix.

Its atrophy continues during the ninth month. At the termination of pregnancy (Fig. 175) it is reduced to 12 or 13 by 10 millimetres in diameter, and its weight to about 500 milligrammes. It is of a faint indefinite hue, but little contrasted with that of the surrounding tissue. The central cicatrix is very small, and appears only as a thin whitish lamina, with radiating processes. The whole mass is still firm to the touch, and readily distinguishable, both from its size and texture, as a prominent feature in the ovarian tissue. The convoluted structure of the external wall is very perceptible, and the point of rupture, with its peritoneal cicatrix, distinctly visible.

FIG. 175.

CORPUS LUTEUM of pregnancy, a term, from a woman dead in delivery from rupture of the uterus.

After delivery, the corpus luteum rapidly retrogrades. At the end of eight days it usually weighs less than 300 milligrammes, and in about two months its color is no longer distinguishable, although indications of its convoluted structure may still be discovered by close examination. These traces of its existence remain for a long time afterward, more or less concealed in the ovarian tissue; being sometimes perceptible so late as nine and a half months after delivery. They finally disappear entirely, together with the external cicatrix which marked their situation.

During pregnancy, owing to the suspension of ovulation and the quiescence of the Graafian follicles, no new corpora lutea are produced; and as those which were formed before the period of conception fade and disappear, the corpus luteum which marks the occurrence of pregnancy after a time exists alone in the ovary.

In twin or triplet pregnancies we should, of course, find a corresponding number of corpora lutea in the ovaries; and it is evident that two Graafian follicles might rupture simultaneously at the time of conception, and but one of the eggs become impregnated or reach maturity. In that case there might be one fœtus in the uterus and two corpora lutea in the ovaries. But in such instances both corpora lutea would be manifestly of the same age and development, and neither of them would resemble the retrograde structures habitually found during menstruation.

After lactation, the ovaries resume their ordinary function. The Graafian follicles mature and rupture as before, and new corpora lutea follow each other in alternate development and disappearance.

The corpus luteum of menstruation, therefore, differs from that of pregnancy in development and duration. While the former passes through all the important phases of its growth and decline in a period of two months, the latter lasts from nine to ten months, and presents, during a great portion of the time, a larger size and more solid organization. Even in the corpus luteum of pregnancy, however, the bright yellow color, which is so striking a feature, is only temporary; not making its appearance till about the end of the fourth week, and again disappearing after the sixth month.

The following table contains, in a condensed form, the characters of the corpus luteum, in menstruation and pregnancy, at different periods of its development:

	Corpus Luteum of Menstruation.	Corpus Luteum of Pregnancy.
At the end of three weeks.	Twelve by nineteen millimetres in diameter; central clot reddish; convoluted wall pale.	
One month.	Smaller; convoluted wall bright yellow; clot still reddish.	Larger; convoluted wall bright yellow; clot still reddish.
Two months.	Reduced to the condition of an insignificant cicatrix.	Twelve by twenty-two millimetres in diameter; convoluted wall bright yellow; clot perfectly decolorized.
Four months.	Absent or unnoticeable.	Eighteen by twenty-two millimetres in diameter; clot pale and fibrinous; convoluted wall dull yellow.
Six months.	Absent.	Still as large as at the end of the second month. Clot fibrinous. Convoluted wall paler.
Nine months.	Absent.	Ten by thirteen millimetres in diameter; central clot converted into a radiating cicatrix; external wall still thick and convoluted, but without any bright yellow color.

CHAPTER VI.

DEVELOPMENT OF THE IMPREGNATED EGG—SEGMENTATION OF THE VITELLUS—BLASTODERM—FORMATION OF ORGANS IN THE FROG.

THE unimpregnated egg has a certain period of growth within the Graafian follicle, during which it increases in size from the insignificant dimensions of its earlier formation to those of its maturity as an ovarian egg. The vitellus, at first transparent and colorless, becomes granular and opaque, at the same time that its mass is enlarged by the deposit of new elements; and in birds and reptiles it also acquires a distinctive hue, generally orange or yellow. These modifications are the result of its spontaneous growth, the materials for which are supplied from the ovarian tissues. At its completion, when the egg is ready to be discharged from the ovary, it consists of the fully formed vitellus, enclosed in a vitelline membrane, and containing, imbedded in its substance, the germinative vesicle with the germinative spot.

Thus constituted, the egg leaves the ovary on the rupture of the ovarian follicle, and enters the Fallopian tube. Here, if coition have taken place, it meets with the spermatozoa, and by their contact and penetration it is made ready for the production of the embryo. It is consequently transformed, by impregnation, from a barren offshoot of the ovarian tissue into a new body, in which the male and female elements are united, and which possesses a capacity for further development.

Immediate Effects of Impregnation.—The first change in the egg, consequent on impregnation, is the disappearance of the germinative vesicle. This feature, always very distinct in the ovarian egg, becomes imperceptible after its contact with the spermatic fluid in the Fallopian tube; and its place is subsequently taken by a new formation, which is designated as the "nucleus of the impregnated egg." The details of this substitution have not been fully ascertained; but its important characters, so far as yet known, are mainly as follows.* The germinative vesicle leaves its position within the vitelline mass and approximates the surface, losing at the same time a portion of its substance, becoming smaller in size and elongated in form. On the other hand, a spermatozoon, which has penetrated into the vitelline sac, becomes also changed by the disappearance of its filamentous portion; and

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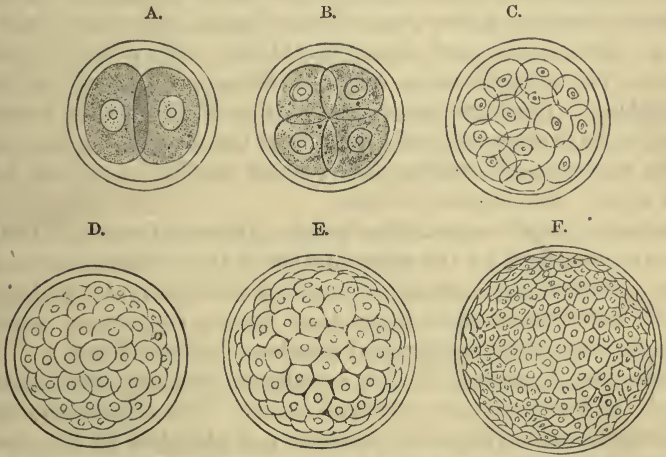
* Kölliker, Embryologie. Paris, 1879, p. 55.

afterward coming in contact with the remainder of the germinative vesicle, the two unite into a single mass. This new product, made up partly of the germinative vesicle and partly of the spermatozoon, then assumes the position and appearance of a central nucleus. It is regarded as the point of origin for all subsequent changes in the impregnated egg.

Deposit of Albuminous Layers in the Fallopian Tube.—As the impregnated egg passes down the Fallopian tube, it becomes covered with an albuminous secretion. In birds, this secretion is deposited in layers round the vitellus, forming the so-called "white of egg." In reptiles, it is also poured out in considerable quantity, and serves for the nourishment of the egg during its development. In mammalians, a similar secretion is supplied in smaller quantity, but sufficiently abundant in proportion to the size of the egg in the earlier stages of its growth, before it has established a connection with the lining membrane of the uterus.

Segmentation of the Vitellus.—A remarkable change now takes place in the impregnated egg, by which its structure is definitely altered. This is known as the division, or "*segmentation*" of the vitellus. Its globular mass is marked by a circular furrow, which gradually deepens until it divides the vitellus into two nearly equal halves or hemispheres. Each hemisphere is then found to contain a nucleus, similar to that which previously occupied the centre of the impregnated vitellus (Fig. 176, A). Almost at the same time a second furrow, at right angles with the first, penetrates the vitellus in a similar way, and cuts it in a transverse direction. The vitellus is thus divided into four equal portions, of a rounded form, lying for the most part in contact with each other and embraced by the vitelline membrane (Fig. 176, B). The

FIG. 176.



SEGMENTATION OF THE VITELLUS, in the impregnated egg of the rabbit. (Coste.)

space existing at certain points between them and the vitelline membrane is occupied by a transparent fluid.

The process thus commenced goes on by the repeated formation of furrows in various directions, dividing the four separated portions successively into eight, sixteen, thirty-two, sixty-four, and so on; until the vitellus is converted into a mulberry-shaped collection of nearly spherical nucleated bodies, resulting from its continued subdivision (Fig. 176, C, D). These bodies are termed the "vitelline spheres." They are of firmer texture than the original vitellus; appearing to increase in consistency as they multiply in numbers and diminish in size. They become at last so abundant as to assume by mutual compression the polygonal form (Fig. 176, E), lying in close contact with each other immediately beneath the vitelline membrane, and surrounding a central space filled with transparent fluid. They are thus converted into a layer of cells, enclosing the original cavity of the egg, and enveloped by the vitelline membrane (Fig. 176, E).

The segmentation of the vitellus is the primary act in the development of the impregnated egg, and the sign that the formation of an embryo has commenced. It takes place in all species of animals, although varying in detail according to the special constitution of the egg and its accessory parts. In all mammalia, as well as in many invertebrates, where the vitellus is very small, and where the body of the embryo immediately after its formation is supplied with nourishment from without, the process is that described above. In birds, in scaly reptiles, and in many fish, where the vitellus is large and contains additional nutritive matter, segmentation takes place only in a thin layer on the surface; and, beginning at one spot, extends outward, advancing more rapidly at the centre of the segmenting region than at its periphery. But in all cases segmentation of the vitellus is the first change in the process of development, and has always the same result, namely, to divide the vitellus into a great number of minute bodies, which present the character of cells.

Blastoderm, or Germinal Membrane.—The cells formed, in the manner above described, by the segmentation of the vitellus, become more closely packed as they increase in number; and finally, by mutual contact and adhesion at their edges, they form a continuous organized membrane, known as the germinal membrane or *blastoderm.*

During the formation of this membrane, the egg, while passing through the Fallopian tube, increases in size. The albuminous matter with which it is enveloped is liquefied and absorbed by the vitelline membrane, furnishing material for the growth of the newly-formed structures. A certain quantity of albuminous fluid also accumulates in the central cavity of the egg.

The next change consists in the appearance in the blastoderm of two separate layers, known as the *external* and *internal blastodermic layers.* They are both still composed exclusively of cells; but those of the external layer are smaller and more compact, those of the internal larger and softer. The egg then has the form of a globular sac, the walls of which consist of three concentric layers, in contact with each other, namely: 1st, the structureless vitelline membrane inclosing the whole; 2d, the external blastodermic layer, composed of cells; and 3d, the internal blastodermic layer, also composed of cells. The cavity of the egg is occupied by an albuminous fluid, absorbed from the exterior and destined to serve as nutritious material.

It is by this process that the simple globular mass of the vitellus is converted into an organized structure. For the blastoderm, although consisting of cells which are nearly uniform in size and shape, is nevertheless a distinct membrane, made up of anatomical elements; and its completion marks the first stage in the formation of the embryo. The blastoderm is in fact the embryo in its primitive condition; and although its texture is at this time exceedingly simple, all the bodily organs are afterward produced by the modification of its different parts. The further process of formation is comparatively simple in some animals, more complicated in others; and its general features are most easily understood by commencing with the study of development as it takes place in the frog.

Formation of Organs in the Frog.—The egg of the frog, when discharged and fecundated, is deposited in the water, enveloped in an albuminous covering of gelatinous consistency. It is thus exposed to the light, the air, and the moderate warmth of the sun's rays, and is supplied with abundance of moisture and nutritious material. Its development is distinguished by a character of great simplicity; since the whole, or nearly the whole, of the vitellus is directly converted into the body of the embryo. There are no accessory organs, and consequently no complications of the formative process.

The two blastodermic layers above described represent the commencement of the new organism. They serve, however, for the production of different parts; and the entire process of development may be concisely expressed as follows:

I. The external blastodermic layer produces the cerebro-spinal axis and the epidermis of the general integument.

II. The internal blastodermic layer produces the epithelium of the alimentary canal and adjacent glandular organs.

III. An intermediate layer, which subsequently appears between the two, produces the vascular tissues, and thus completes the constitution of the bodily frame.

The first sign of advancing organization in the blastoderm shows itself in a thickening and condensation of its structure. The thickened portion has the form of an elongated spot, termed the "embryonic spot" (Fig. 177), the wide edges of which are more opaque than the adjacent parts. Between these opaque edges is a narrower, colorless, and transparent space—the "area pellucida," within which is a delicate line, running longitudinally from front to rear, called the "primitive trace."

In the anterior portion of the area pellucida, the substance of the blastoderm rises up in such a manner as to form two nearly parallel ridges or plates, which approach each other from side to side, over what will be the dorsal aspect of the embryo, and are therefore called the "dorsal plates." Between them is included a groove, termed the "medullary groove." The dorsal plates afterward meet and coalesce on the median line, thus converting the intervening groove into a canal. The coalescence of the dorsal plates takes place first in the anterior part of the area pellucida, extending thence gradually backward; and when it is complete the whole of the medullary groove becomes a closed canal. This is the "medullary canal;" and within it is formed the cerebro-spinal axis, by a growth of nervous matter from its internal surface. At its anterior extremity, the medullary canal is large and rounded, producing the brain and medulla oblongata; its remainder is narrow, and pointed posteriorly, corresponding in form with the future spinal cord. At the same time, the thickened edges of the blastoderm grow outward and downward, extending over the lateral portions of the vitelline mass. They are called the "abdominal plates;" and they approach each other below enclosing the abdominal cavity, as the dorsal plates above enclose the medullary canal. At last they unite on the median line, embracing the whole of the internal blastodermic layer, which encloses in turn the remains of the vitellus and the albuminous fluid contained in its cavity.

Fig. 177.

Diagrammatic view of the Impregnated Egg, showing the embryonic spot, area pellucida, and primitive trace.

Simultaneously with these changes, there is formed, in the thickened central part of the blastoderm, immediately beneath the medullary canal, a longitudinal, cylindrical cord—the "chorda dorsalis." Around the chorda dorsalis are afterward developed the bodies of the vertebræ, the oblique processes of the vertebræ running upward into the dorsal plates, while the transverse processes and ribs run outward and downward in the abdominal plates, to encircle more or less completely the corresponding portion of the body.

In a longitudinal section of the egg, during this process, the thickened portion of the external blastodermic layer (Fig. 178, $_1$) may be seen in profile. The anterior portion ($_2$), which will form the head, is thicker than the posterior ($_3$), which will form the tail. As the whole mass grows rapidly, in both the anterior and posterior direction, the head becomes thick and voluminous, while the tail begins to project backward, and the egg assumes an elongated form. (Fig. 179.) The abdominal plates also meet upon its under surface, and complete the closure of the abdominal cavity. The internal blastodermic layer is embraced by the abdominal plates, enclosing, as before, the remains of the vitellus.

As development goes on (Fig. 180), the head becomes larger, and shows traces of the organs of special sense. The tail also increases in size, and projects farther from the posterior extremity of the embryo. The spinal cord runs in a longitudinal direction from front to rear, and its anterior extremity enlarges, to form the brain and medulla oblongata. In the mean time, the internal blastodermic layer, subsequently converted into the epithelium of the intestinal canal, has been shut in by the abdominal walls, and forms a closed sac, of slightly elongated figure, without inlet or outlet. Afterward, the mouth is formed by a perforation through both external and internal layers at the anterior extremity; while a similar perforation, at the posterior extremity, results in the formation of the anus.

Fig. 178.

Diagram of Frog's Egg, in an early stage of development; longitudinal section.—1. Thickened portion of external blastodermic layer. 2. Anterior extremity of the embryo. 3. Posterior extremity. 4. Internal blastodermic layer. 5. Cavity of vitellus.

Fig. 179.

Egg of Frog, in process of development.

Fig. 180.

Egg of Frog, farther advanced.

Fig. 181.

Tadpole, fully developed.

By a continuation of the same process, together with the development of the intermediate vascular layer, the different portions of the body are gradually constructed, producing the skeleton, the integument, the organs of special sense, and the muscles and nerves. The tail acquires sufficient size and strength to be capable of acting as an organ of locomotion (Fig. 181). The intestinal canal is at first a short, wide, nearly straight tube, running directly from the mouth to the anus. It then begins to grow faster than the abdominal cavity which encloses it, becoming longer and narrower, and at the same time thrown into numerous curvilinear folds.

Arrived at this period, the young tadpole ruptures the vitelline membrane, and leaves the cavity of the egg. He at first attaches himself to the remains of the albuminous envelope, and feeds upon it for a short time. He soon, however, acquires sufficient strength and activity to swim about in search of other food, propelling himself by his large, membranous, and muscular tail. The alimentary canal increases in length and becomes spirally coiled in the abdominal cavity, attaining a length from seven to eight times greater than that of the entire body.

Afterward, a change takes place in the external form of the animal. The posterior limbs are the first to make their appearance, by budding or sprouting from the sides of the body at the base of the tail. The anterior extremities are for a time concealed beneath the integument, but afterward become liberated, and show themselves externally. At first both the fore and hind legs are very small, incomplete in structure, and useless for locomotion. They subsequently increase in size and strength; while the tail, on the contrary, ceases to grow, and becomes shrivelled and atrophied. The limbs, in fact, are destined to replace the tail as organs of locomotion; and a time at last arrives when the tail has altogether disappeared while the legs are fully developed, muscular, and powerful. Then the animal, heretofore confined to an aquatic mode of life, becomes capable of living on land, and the tadpole is transformed into the frog.

During the same time, other changes take place in the internal organs. The tadpole at first breathes by gills; but these organs subsequently become atrophied, and are replaced by lungs. The structures of the mouth, of the integument, and of the circulatory system, are altered to correspond with the varying conditions of the growing organism; and these transformations, taking place in part successively and in part simultaneously, bring the body at last to a state of completion.

The development of a young animal from the egg consists therefore of a series of changes, in which different organs make their appearance from modifications of the blastoderm. Many of these organs are temporary, serving for the growth of the embryo during a certain period; while others are of more permanent structure, and, after passing through various alterations of size and form, become component parts of the adult organism.

CHAPTER VII.

FORMATION OF THE EMBRYO IN THE FOWL'S EGG.

THE process of embryonic development in the egg of the bird differs from that of the frog in two important particulars. First, the whole of the vitellus, or yolk, in the bird's egg, is not directly converted into the body of the embryo, but a large part is transformed into a nutritious fluid, and thus serves indirectly for its growth. Secondly, certain accessory organs make their appearance, extending beyond the limits of the body of the embryo, and surrounding it with membranous envelopes. The development of the chick, during incubation, has been found especially favorable for the study of many details as to the formation and growth of the various organs; and some of the most valuable discoveries in embryology have been obtained in this way.

The Yolk and the Cicatricula.—The yolk of the fowl's egg represents something more than the vitellus proper. Its principal mass consists of an opaque, yellow, semifluid substance, the "yellow yolk," which solidifies on boiling, owing to its large proportion of albuminous matter. This substance contains an abundance of soft, spherical, finely granular bodies, from 25 to 100 mmm. in diameter.

The yellow yolk is everywhere surrounded by a thin nearly colorless layer, the "white yolk," which contains, instead of the granular spheres above described, smaller globular bodies with one or more brightly refracting masses in their interior. The albuminous matter of the white yolk, furthermore, does not solidify firmly on the application of heat; so that in a boiled egg the thin stratum of this substance remains semifluid. There is also a spot at the centre of the yolk, which is occupied by the same material, and which consequently remains soft in the boiled egg; the cavity thus left communicating with the surface of the yolk by a narrow passage, like the neck of a flask.

The yolk is thus formed of two substances, distinguished by their microscopic characters and by their comparative coagulability at the boiling temperature. Neither of these substances corresponds with the granular vitellus of the mammalian egg; they constitute a deposit of nutritious material, destined for the support of the embryonic tissues.

At one point on the surface of the yolk, in the unfecundated egg, is a whitish circular spot, about three millimetres in diameter, immediately beneath the vitelline membrane. This is the *cicatricula.* It is a thin layer, of minutely granular structure; its granules being imbedded in a homogeneous substance by which they are agglutinated into a disk-like mass. In its centre is the germinative vesicle, distinctly visible by its transparency and well defined outline, and marked, in the ovarian egg, by a germinative spot. According to Kölliker, the germinative spot disappears before the mature yolk is discharged from the ovary; and it is consequently not visible in the egg in the oviduct.

The cicatricula is the only part of the fowl's yolk which undergoes segmentation, and which is directly concerned in the production of the embryo. It corresponds therefore with the vitellus of the mammalian egg, and has received the name of the "plastic" or formative vitellus; while the remainder, consisting of the white and yellow yolk, is known as the "nutritive" vitellus. The position of the cicatricula is immediately above the tubular prolongation of white yolk leading to the central cavity of the egg.

Segmentation in the Fowl's Egg, and Formation of the Blastoderm.—The fowl's egg is fecundated soon after leaving the ovary, in the upper portion of the oviduct. Segmentation begins in the lower half of the oviduct and goes on during the production of the shell membranes and shell; and in the new-laid egg the formation of the blastoderm is usually complete.

The process of segmentation in the fowl's egg differs from that already described (page 617) in the following particulars: Instead of a globular vitellus successively bisected into smaller spheres and hemispheres, there is a flattened vitelline disk, the cicatricula, which is cut by superficial furrows, running in various directions, and dividing its area into a number of spaces by their intersection. The principal furrows radiate from the central part of the cicatricula, and are united at irregular intervals by cross furrows, which mark off isolated portions of its substance. The cicatricula is thus broken up into a large number of segments; but this segmentation takes place by extension over a flattened surface, spreading gradually from the centre outward, instead of affecting at once the whole vitellus, as in the mammalian egg.

The details of segmentation in the fowl's egg have been most fully studied by Coste* and Kölliker.† It begins by the appearance of a straight or curvilinear furrow, crossing the middle portion of the cicatricula without reaching to its edges, and dividing it imperfectly into two nearly equal halves (Fig. 182, I.). This furrow is afterward crossed at right angles by a second, dividing the disk into four sectors (Fig. 182, II.). The point, however, at which the sectors meet is not usually the exact centre of the cicatricula, but a little on one side; and the whole process of segmentation, according to Kölliker, goes on in such a way that its point of greatest activity is always somewhat eccentric in position. The primary furrows thus formed are followed by others which radiate toward the edges of the cicatricula, while its central parts are broken up, as above described, into smaller

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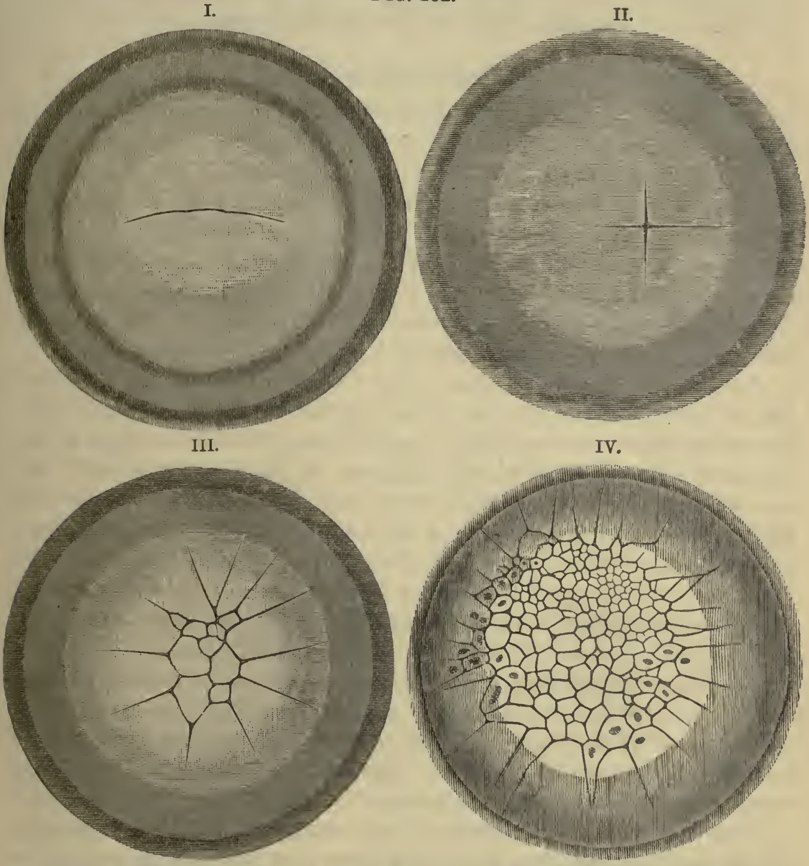
* Histoire Générale et particulière du Développement des Corps organisés. Paris, 1847–59. Poule, Pl. ii., Figs. 7–13.

† Embryologie. Paris, 1879, p. 63–85.

segments by transverse and oblique furrows of communication (Fig. 182, III.). By the continuance and peripheral extension of this process the area of segmentation is gradually divided into small polygonal bodies (Fig. 182, IV.), many and finally all of which are provided with a central nucleus, and which are accordingly regarded as nucleated cells.

The study of perpendicular sections of the cicatricula in this condition shows that its segmentation extends not only in a lateral direction, but also throughout its depth. The furrows which appear to divide it into isolated parts are at first only superficial, and its surface is already subdivided while its deeper portions are still entire. But the process of division continues from above downward until it occupies the whole thickness of the plastic vitellus, to the surface of the white yolk. By this means the cicatricula is converted into a disk-like mass of nucleated cells, and is then known as the "blastoderm."

Fig. 182.



Phases of Segmentation in the Cicatricula of the Fowl's Egg, within the oviduct. (Kölliker.)

In the new-laid egg, the blastoderm is already composed of two layers. The external layer, at this time the more completely formed of the two, consists in its central portions of closely packed cylindrical cells, in several superimposed ranges; and toward its outer borders of a single range of flattened cells, placed edge to edge. The internal layer consists of rounded cells, more coarsely granular than those of the external layer, and less closely consolidated into a continuous mass. This is the condition of the blastoderm in the fecundated fowl's egg, at the time of its discharge from the generative passage.

Incubation of the Egg and Formation of the Embryo.

When the fecundated egg is discharged from the generative passage and allowed to cool, the process of development is suspended at the point above described. The formative changes in the blastoderm require for their accomplishment a warmth nearly equal to that of the fowl's body, namely, about 40° C.; and the egg, if kept at lower temperatures, may remain inactive for a considerable time without losing its vitality. When the necessary warmth is again supplied, by natural or artificial incubation, development recommences and goes on to the formation of the embryonic tissues.

Extension of the Blastoderm.—The first modification in the egg during incubation is the increase in size of the blastoderm. This membrane has already become larger than the cicatricula from which it was produced; for while the average diameter of the cicatricula before segmentation is about three millimetres, the blastoderm in the new-laid egg measures from three and a half to four millimetres (Kölliker). But when incubation commences, it expands so rapidly that in twenty-four hours it is 11 or 12 millimetres in diameter, and by the end of the second day it reaches twice that size. By the continued expansion of its borders it covers more and more of the spherical yolk, passing after a time the equatorial line and approaching its opposite pole. At the end of the fourth day there is only a small space which it has not yet covered, and by the sixth day it has completely enveloped the yolk in a sac-like, membranous extension. The nutritive vitellus is thus finally enclosed by the expanding blastoderm.

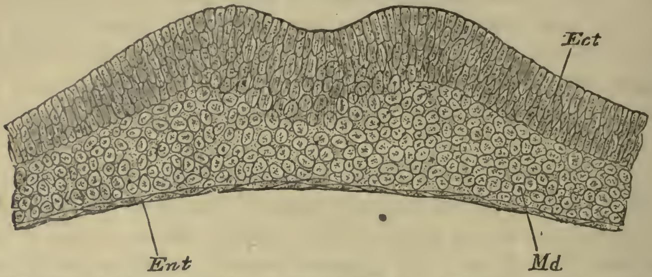
Area Pellucida and Primitive Trace.—The next most striking feature of the incubated egg is the appearance, at the central part of the blastoderm, of the circular spot, known as the "area pellucida." It is so called from its transparent appearance, due to the uniform structure and close approximation of the cells of the external blastodermic layer in this situation. The area pellucida occupies about one-half the extent of the whole blastoderm, which is at this time from four to five millimetres in diameter. It is surrounded by the remaining non-transparent portion of the blastoderm, the "area opaca," the opacity of which is due to the fact that its internal blastodermic layer, formed of large, loosely packed and rounded cells, is two or three times as thick as the external layer. In the area pellucida, on the contrary, the principal thickness of the blastoderm is formed by the external layer; the internal consisting of only a single range of cells, often incompletely continuous. As the blastoderm enlarges, its area pellucida encroaches on the space previously occupied by the area opaca; and the area opaca expands in turn, advancing beyond the borders of the transparent portion. The area pellucida soon assumes an oval form, placed transversely to the long axis of the egg; and the body of the embryo will afterward occupy the same position, the wider end of the oval corresponding to the future situation of the head, its narrower end to that of the tail.

Not long after the formation of the area pellucida, it presents in its longitudinal axis a slight linear eminence, caused by local thickening and condensation of the external blastodermic layer. This is known as the "primitive trace." It appears, from the tenth to the fourteenth hour of incubation, as an ill-defined linear opacity, about one millimetre in length and 0.2 millimetre in width, of a straight or slightly sinuous form, and somewhat eccentric in position, occupying rather the posterior than the anterior portion of the area pellucida. It shows, along the median line on its upper surface, a shallow depression, the "primitive furrow," and by the fifteenth hour of incubation it is fully constituted in all its parts.

The primitive trace, although it indicates the direction of the longitudinal axis of the future embryo, is not an initial formation of the embryonic organs, and takes no direct part in their development. It is a transitory structure, which disappears soon after its production, and gives place to others of more permanent significance. But it is a feature of much interest, as the earliest local modification in the transparent portion of the blastoderm.

Formation of Three Blastodermic Layers.—The blastoderm, at the time of its appearance in the new-laid egg, consists, as above described, of two layers of cells, namely, an external and an internal. Of these, the external alone is fully constituted; the internal being less complete and more or less discontinuous in the central portions of the blastoderm. But a few hours after the commencement of incubation, the internal blastodermic layer becomes continuous throughout, forming everywhere a distinct consistent expansion. Within the limits of the area pellucida its cells assume a flattened form, being thus still further distinguished from those of the external layer, which in this situation are more cylindrical in figure and multiply with great rapidity. Soon afterward a third blastodermic layer makes its appearance, between the other two, composed of uniformly rounded cells. It is first produced along the line of the primitive trace, and thence extends laterally on each side, diminishing in thickness until it terminates, at some distance from the median line, in a thin edge. In the region of the primitive trace (Fig. 183) the blastoderm is then composed of three cellular layers, which have received distinct names, and which afterward give origin to all the organs of the embryo, namely: 1st, the external blastodermic layer, or *Ectoderm*, which produces the cerebro-spinal axis and the tegumentary epidermis; 2d, the internal layer, or *Entoderm*, producing the intestinal and glandular epithelium; and 3d, the intermediate layer, or *Mesoderm*, from which the great mass of the muscular system, the blood and circulatory apparatus, and the vascular tissues in general are subsequently developed.

FIG. 183.



TRANSVERSE SECTION OF BLASTODERM OF FOWL'S EGG, at the situation of the primitive trace and primitive furrow. *Ect*, Ectoderm. *Md*, Mesoderm. *Ent*, Entoderm. (Kölliker.)

Folds of the Blastoderm.—The form of the embryo and its different parts is sketched out, in all cases, by a series of folds, which show themselves at various points in the blastoderm. This membrane presents at first a flat surface; or, if it have a certain degree of convexity, corresponding with that of the yolk upon which it lies, this convexity is perfectly uniform, and too slightly pronounced to be appreciable within the limits of the blastoderm. But as soon as development begins to make definite progress, this uniformity of surface is broken by the appearance of transverse and longitudinal folds, forming lines of separation between different parts of the blastoderm. Such a fold, running in a curvilinear direction from side to side, marks the position of the head of the embryo, and is called the "head-fold." Its free border, projecting above the neighboring portion of the blastoderm, becomes the head, which, as well as the neck, is curved forward and downward, in the subsequent stages of growth, with the deepening of the fold which first gave it origin as a distinct part. A similar fold at the posterior portion of the area pellucida, marks off the hinder extremity of the embryo, and is called the "tail-fold." Longitudinal folds, formed in the same manner on each side, fix the lateral limits of the body of the embryo.

By this means a certain portion of the blastoderm becomes marked off from the rest. The part included within the transverse and longitudinal folds is the body of the embryo; while that remaining outside these limits becomes developed into accessory organs, playing an important but secondary part in the history of development. Similar folds of the blastoderm also make their appearance within the body of the embryo, and are the principal means of formation for its different organs. A pair of longitudinal ridges, adjacent to the median line, form the two halves of the cerebro-spinal axis, which afterward coalesce with each other along their dorsal edges; and the formation of the intestinal canal, as well as its inclosure by the abdominal walls, results from the growth of lateral folds which curve downward and inward, to meet on the median line below. Thus the body of the embryo, consisting mainly of the thickened ectoderm and mesoderm, is at first spread out, in a nearly uniform plane, over the surface of the yolk, resting upon the entoderm, which represents the epithelial lining of its future alimentary canal. But as the depressed folds of its lateral borders penetrate more deeply below the general level, the sides of the embryo shut in between them a cavity, which is afterward completed by the union of its edges, and thus finally embraces the alimentary canal, with the other thoracic and abdominal organs.

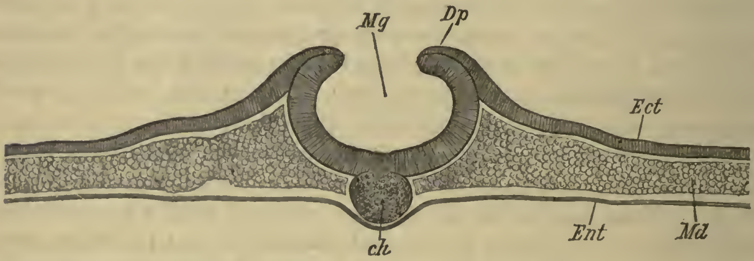
The above changes, which thus determine the configuration of the embryo, result from the special activity of growth in particular parts of the blastoderm. If this membrane were to grow only at its edges, it would simply extend farther over the vitellus, its central portions remaining as before. If it were to increase everywhere at a uniform rate, it would become thicker as well as more extensive, but without any special alteration of form. This is what really takes place during the early production of the blastoderm, which at first expands on all sides, retaining its original uniformity of surface.

But with the commencement of incubation the blastoderm grows more rapidly at particular points, and along certain lines, than elsewhere. What may be the determining cause of such a concentration of growth, it is impossible to say; but its result is that the blastoderm, enlarging with different degrees of rapidity in different regions, is thrown into undulations, which indicate, by their position and size, the unequal expansion of its mass. Thus, if it grow more rapidly at one point than in the adjacent parts, it will form at that spot either an eminence or a depression, according as it meets with less resistance above or below. If a similar rapidity of increase should take place along a transverse line, the consequence would be a transverse fold; and if in an antero-posterior direction, it would cause a longitudinal fold. The subsequent history of embryonic development shows continual repetitions of this process, often on a much larger scale than in the blastoderm. The folds of the intestinal canal, the valvulæ conniventes of its mucous membrane, the convolutions of the brain, and the tubular windings of the perspiratory glands, with many other analogous forms, are produced in a similar way. All these structures are at first smooth or straight. They become thrown into folds or convolutions during the development of the embryo, whenever they grow more rapidly than the surrounding parts.

Position of the Embryo in the Egg.—Although the blastoderm is at first apparently of uniform structure throughout, yet each particular part has from the beginning a physiological individuality, which leads to its subsequent development into a special organ or part of an organ.

This is evident from the manner in which the local activity of nutrition gives rise to the appearance of folds, running in definite directions, and determining in this way the future location of the head, the tail, and the sides of the body. But it is manifested still more remarkably in the position of the entire embryo. The yolk of the fowl's egg has a nearly regular spherical form; and the cicatricula, as well as the blastoderm into which it is converted, is a circular spot upon its surface. The ovoid form presented by the whole egg, with one round and one pointed extremity, results from the deposit of albumen around the yolk, in the middle and lower parts of the oviduct, after fecundation has taken place. But when the rudimentary embryo first becomes perceptible in the area pellucida, it is so placed in the large majority of instances as to lie crosswise to the long axis of the egg, with its left side toward the round end and its right side toward the pointed end. Even before incubation has commenced, one particular portion of the circular blastoderm is destined to become the head and another portion the tail; and consequently every one of the future organs of the embryo has its point of origin already fixed.

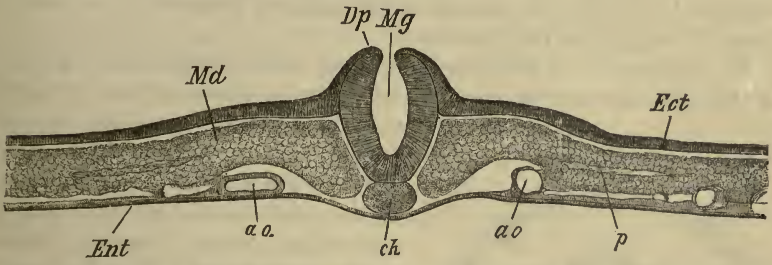
Fig. 184.



Transverse Section of Embryo Chick, second day of incubation, through open portion of medullary groove.—*Mg.* Medullary groove. *Dp.* Dorsal plates. *Ch.* Chorda dorsalis. *Ect.* Ectoderm. *Md.* Mesoderm. *Ent.* Entoderm. Magnified 83 times. (Kölliker.)

Dorsal Plates, Medullary Canal, and Cerebro-Spinal Axis.—During the first day of incubation the primitive trace is bordered on each side and around its two extremities by a thickened extension of the blastoderm, which rapidly assumes an elongated form and grows more rapidly in the anterior than in the posterior direction. Early in the second day there appear, within the embryonic spot, in front of the primitive trace, two parallel longitudinal folds of the ectoderm, which project above the surface, leaving between them, along the median line, a corresponding longitudinal depression (Fig. 184). These ectodermic folds are known as the "dorsal plates," and the depression between them is the "medullary groove." As the dorsal plates increase in height, their edges curve inward, and the intervening groove, which is lined with the cells of the ectoderm, becomes deeper and more capacious. By a continuance of this process, the edges of the dorsal plates are more closely approximated, and the medullary groove, at first widely open along the dorsal surface, is reduced at its opening to a comparatively narrow fissure (Fig. 185).

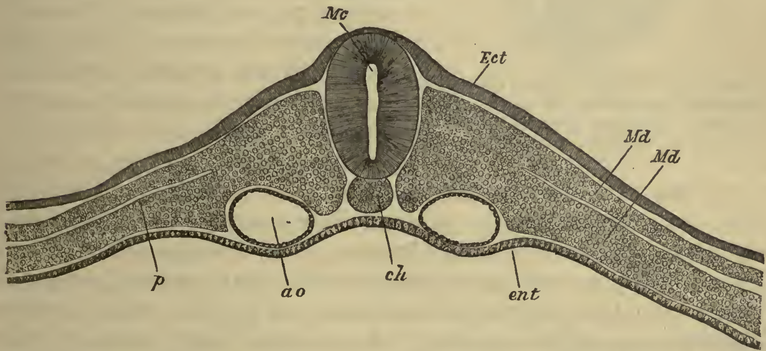
FIG. 185.



Transverse Section of Embryo Chick, through narrowed portion of medullary groove.—*Mg.* Medullary groove. *Dp.* Dorsal plates. *Ect.* Ectoderm. *Md.* Mesoderm. *Ent.* Entoderm. *Ch.* Chorda dorsalis. *p.* Peritoneal space. *a o.* Embryonic aorta, one on each side. (Kölliker.)

That the dorsal plates are formed, in the manner above described, by folds of the ectoderm, is plain from the fact that at this time the layer of ectodermic cells lining the medullary groove is reflected continuously on each side, at the edges of the dorsal plates, upon the adjacent free surface of the blastoderm. Finally, the dorsal plates come in contact at their edges and coalesce with each other, thus obliterating the fissure between them, and converting the medullary groove into a closed canal (Fig. 186). When this change is accomplished, the ectoderm, which was originally continuous throughout, is divided into two portions—a thicker portion lining the cavity of the canal, and a thinner portion covering the canal along the median line and thence extending laterally over the general surface of the blastoderm. The canal thus formed is the "medullary canal." The layer of cells by which it is surrounded afterward produces the brain and spinal cord, or the

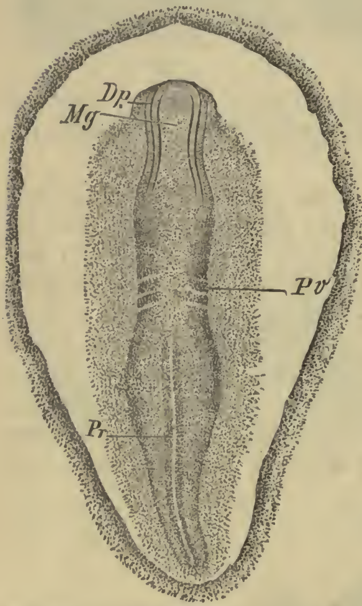
FIG. 186.



Transverse Section of Embryo Chick, through closed portion of medullary canal.—*Mc.* Medullary canal. *Ect.* Ectoderm. *Ent.* Entoderm. *Md. Md.* Outer and inner laminæ of Mesoderm. *p.* Peritoneal space. *ch.* Chorda dorsalis. *a o.* Aorta.

cerebro-spinal axis; and the canal itself becomes, in the adult, the central canal of the spinal cord, with its continuations in the encephalon, namely, the fourth ventricle, aqueduct of Sylvius, and third ventricle. The external portion of the ectoderm, remaining outside the medullary canal and covering the surface of the embryo, becomes the epidermic layer of the general integument.

FIG. 187.



RUDIMENTARY EMBRYO OF THE CHICK, at the thirtieth hour of incubation. *Pr.* Proto-vertebræ. *Dp.* Dorsal plates. *Mg.* Medullary groove. *Pr.* Primitive trace. (Kölliker.)

The coalescence of the dorsal plates, by which the medullary groove is converted into a canal, does not take place at the same time throughout. It is first completed in the middle portion of what will afterward be the head; the anterior part of the encephalon, and the cervical and dorsal portions, remaining open until a later period. Their final closure proceeds in a general direction from before backward, occupying successive portions as development goes on, and reaching at last the posterior extremity.

The dorsal plates, as the immediate precursors of the cerebro-spinal axis, are the first distinct indication of a permanent embryonic organ. Their relation to the primitive trace is not very well defined, and it is doubtful whether they are especially connected with its formation. They first appear in advance of its anterior extremity; and, although the medullary groove between them corresponds in its general longitudinal direction with the median furrow of the primitive trace, the two are not uniformly continuous, but, according to Kölliker,* are often laterally displaced, the one falling a little to the right, the other to the left. The medullary groove is moreover considerably wider than the primitive furrow; and, while the cephalic region of the embryo, as well as its cervical and dorsal portions, grow very rapidly with the progress of incubation, the primitive trace remains confined to the caudal extremity. Its greatest length, about the thirtieth hour of incubation, is rather less than two millimetres; it begins to diminish perceptibly from the fortieth to the forty-second hour, and at the end of the second day has almost disappeared. By this time the medullary canal is closed for nearly the whole length of the cerebro-spinal axis.

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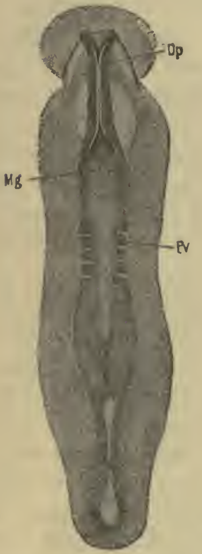
* Embryologie. Paris, 1879, pp. 109, 141.

Protovertebræ, Chorda Dorsalis, and Vertebral Column.—On the first appearance of the dorsal plates and medullary groove, at the beginning of the second day of incubation, these structures occupy the anterior half of the rudimentary embryo, or that portion which will afterward become the head. Immediately behind this region, and slightly in front of the primitive trace, a transverse division becomes apparent on each side at a little distance from the median line. This division, though visible externally as a transparent line, is really situated in the mesoderm, the cells of which undergo disintegration at this point along a transverse plane, thus causing a separation between its anterior and posterior portions. A second line of division soon follows, parallel to the first and about 0.75 millimetre behind it, including between the two a nearly rectangular mass of the body of the embryo. Almost immediately a third line appears in advance of the first; and by this means there are formed on each side two well-defined quadrangular sections of the mesoderm. (Fig. 187.) They are the precursors of a longitudinal chain of similar divisions, appearing successively from before backward, until in the fourth day of incubation they form a series of twenty-one or twenty-two pairs. From their early appearance and their resemblance to the articulations of the future vertebral column, they have received the name of the "protovertebræ."

The protovertebræ first formed correspond in situation with the anterior cervical region of the embryo. The second pair, in the order of formation, is placed in advance of the first; while the third pair appears immediately behind it. (Fig. 188.) At this time the closure of the dorsal plates has taken place throughout the middle portion of the head, while in the anterior and posterior cephalic regions the medullary groove is still open. In the cervical region, where the protovertebræ are being formed, this groove has but little depth; and farther back, near the situation of the primitive trace, it is wider and shallower still. As additional protovertebræ become visible at the end of the series, those of latest formation are always at the same distance in front of the primitive trace. This shows that they are formed from new material supplied by a rapid growth of the blastoderm in this situation; each protovertebra taking the place of that which preceded it in the order of formation, but falling behind in the linear series. In an embryo showing seven or eight pairs of protovertebræ, as in Fig. 189, the last pair is still considerably in advance of the caudal extremity; and the remaining pairs, belonging to the dorsal region, are still to be formed by the same process. At this time the medullary canal is closed throughout its cephalic portion, but is still open in the cervical region at the level of the third pair of protovertebræ. From this point backward it becomes gradually shallower and wider, expanding to its greatest width in the caudal region, where it embraces the anterior extremity of the primitive trace. When the protovertebræ have reached their full number, at the forty-eighth or fiftieth hour of incubation, the caudal portion of the medullary groove still extends a certain distance beyond them, and they are also absent from the region of the head.

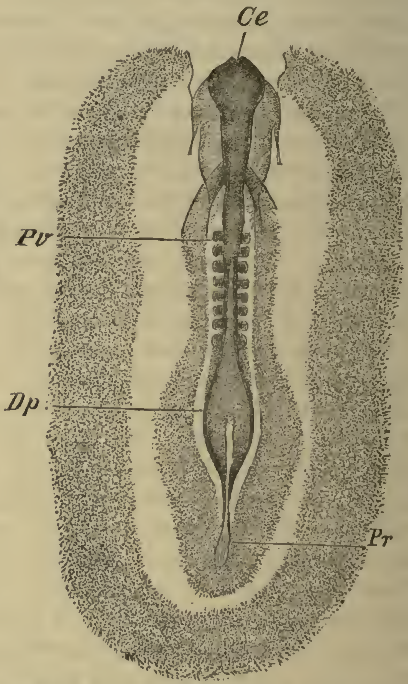
The subsequent history of the protovertebræ consists in their transformation into other tissues and their final disappearance as distinct organs. Their upper and outer portions are mainly converted into the voluntary muscles covering the spinal column, while their inferior and inner portions supply the material for the bodies of the vertebræ, the vertebral arches, and the intervertebral ligaments. During this process they become, for the most part, fused with each other in the longitudinal direction, and by the end of the fifth day the divisions between them are no longer visible.

Fig. 188.



Rudimentary Embryo of the Chick, at the thirty-sixth hour of incubation. *Dp.* Dorsal plates, cephalic region. *Mg.* Medullary groove. *Pv.* Anterior pair of protovertebræ. (Kölliker.)

Fig. 189.



Embryo of Chick, about the fortieth hour of incubation. *Ce.* Cephalic extremity. *Pv.* Protovertebræ. *Dp.* Dorsal plates, still widely separated in the caudal region. *Pr.* Primitive trace. (Kölliker.)

The *chorda dorsalis*, already mentioned (page 620), is a slender longitudinal cylinder, rather less than 0.1 millimetre in diameter, situated in the median line, between the ectoderm and entoderm, immediately beneath the medullary canal. It first appears, from the twentieth to the twenty-fourth hour of incubation, at the posterior part of the medullary groove. It thence extends forward, during the second day, to a point corresponding with the middle region of the head. It is composed of uniformly rounded cells agglutinated with each other, as shown in Figs. 184, 185, 186.

During the third day the inner and lower portions of the protovertebræ extend toward the median line in such a manner as to surround the chorda dorsalis, above, below, and on each side, with an investment of new material. As these newly formed portions of the protovertebræ coalesce with each other, the chorda dorsalis becomes covered with a continuous tubular sheath, or investing membrane. This forms a rudimentary vertebral column; since the substance of the sheath, in the further progress of growth, becomes first cartilaginous and afterward bony, producing finally the bodies of the vertebræ.

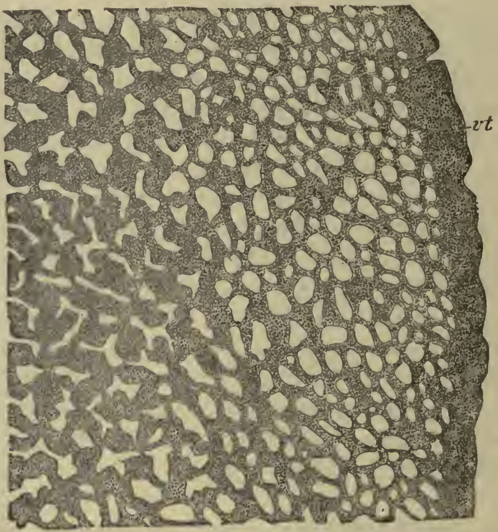
While the sheath of the chorda dorsalis is thus formed from the inner and lower portions of the protovertebræ, their inner and upper portions extend, as a thin expansion on each side, between the medullary canal and the tegumentary layer of the ectoderm. On the fourth day these lateral growths meet and coalesce at the median line, on the dorsal aspect of the embryo; and the embryonic spinal cord is then enclosed in a membranous investment, similar to that of the chorda dorsalis. In this investment there are afterward formed the oblique processes of the vertebræ, which, by uniting with each other in the same way on the median line, finally enclose the cerebro-spinal axis in a series of vertebral arches. The deposit of cartilaginous matter, in the double membranous tube thus formed, takes place at successive points in a linear series; and from each point the cartilaginous deposit, as well as its subsequent ossification, extends gradually to its final limit. The intervening portions, not converted into cartilaginous and bony tissues, become, between the bodies of the vertebræ, the intervertebral ligaments, and between the dorsal arches the yellow ligaments of the vertebræ.

But in this transformation of a portion of the protovertebræ into a permanent spinal column, the final arrangement of the parts is different from that at the beginning. When the cartilages of the permanent vertebræ make their appearance, they do not correspond in situation with the original protovertebræ. Subsequently to the fusion of the protovertebræ with each other, a new segmentation takes place, the lines of division passing through the former intervening spaces. Each permanent vertebra therefore corresponds in position with the adjacent halves of two protovertebræ; and the middle portion of each protovertebra is finally replaced by an intervertebral ligament.

Area Vasculosa, Blood and Blood-vessels.—The mesoderm, during the earliest periods of incubation, is less rapid in its lateral extension than the two other blastodermic layers; but it undergoes important changes in texture, which lead to the development of the vascular system. This begins in the second day. Within the body of the embryo at this time the mesoderm exhibits on each side, at some distance from the median line, a horizontal cleft (Fig. 185, *p*), by which it is divided into two laminæ, one above, contiguous to the ectoderm, and one below, next the entoderm; and a little later (Fig. 186) the division between them is more complete. This cleft represents the future peritoneal cavity. The external lamina of the mesoderm will afterward supply the voluntary muscles and other tissues of the thoracic and abdominal walls; while the involuntary muscular layer of the alimentary canal is derived from its internal lamina. Outside the body of the embryo the internal lamina increases in thickness, and becomes of great importance in the formation of the blood and blood-vessels.

The first appearance of vascularity shows itself, early in the second day, in the parts immediately surrounding the area pellucida. Certain spots in the mesoderm of this region assume the form of irregularly-shaped spaces filled with red blood globules, which soon unite with each other in such a way as to form a network of inosculating vessels. The region of the blastoderm occupied by this network is known as the "area vasculosa." There is at first no arrangement of the blood-vessels in trunks and branches, nor any apparent distinction corresponding to that of arteries and veins. All are of nearly the same size, distributed on the same plane and communicating equally with each other; except that they are surrounded by a large vessel, the "vena terminalis," with which all the adjacent vessels communicate and which thus forms the exterior limit of the vascular area (Fig. 190). Subsequently a difference shows itself in the extent and rapidity of their growth, some preponderating in size over the others; and by the end of the third day there is a visible distinction between their trunks, branches, and ramifications. At the same time the formation of blood-vessels extends

Fig. 190.

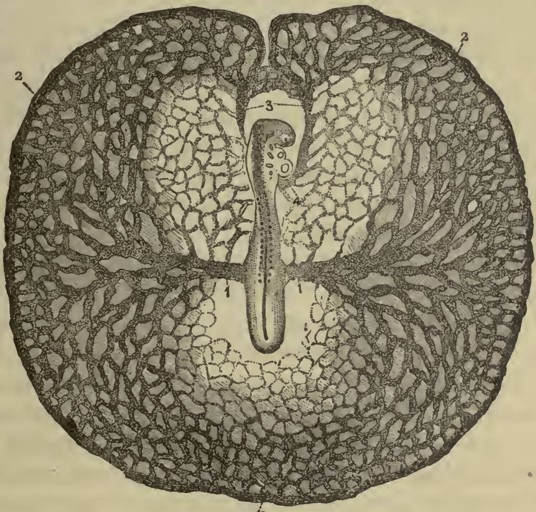


Portion of the Vascular Area, from the blastoderm of the chick at the fortieth hour of incubation, showing islets of blood and embryonic blood-vessels. *Vt.* Vena terminalis. (Kölliker.)

from without inward, occupying successively different parts of the area pellucida, and finally reaching the body of the embryo, into which they penetrate by its lateral edges.

The main features of the development of the blood and blood-vessels are as follows: First. Their formation commences in what afterward becomes the area vasculosa; that is, a part of the blastoderm lying on the surface of the yolk outside the body of the embryo. Secondly. The walls of the newly-formed vessels, when they first become pervious to the blood, consist of a single layer of flattened cells, representing the endothelium of the adult blood-vessels. These endothelial tubes extend by budding and proliferation through the area pellucida into the body of the embryo, where they become continuous with the endothelial lining of the embryonic blood-vessels and heart; and the muscular and fibrous coats, of the heart and blood-vessels everywhere, are afterward produced by a development of new tissue around the primitive vascular channels. Thirdly. The first movement of red blood is from the area vasculosa toward the embryo. For the heart, when its pulsations begin, during the second day of incubation, contains only a colorless fluid; the red globules being then accumulated in the place of their formation, that is, the meshes of the area vasculosa. But by the movement of the colorless plasma, under the impulsive force of the heart's action, the red globules become detached from their resting-places and gradually mingled with the circulating current.

Fig. 191.



Area Vasculosa of the Embryo Chick, after three and a half days of incubation. 1, 1. Vitelline arteries. 2, 2, 2. Vena terminalis. 3. Anterior vitelline veins, right and left. 4. Right lateral vitelline vein. From preparations by Prof. William Hailes.

When the system of the area vasculosa is fully established, on the third day of incubation, the body of the embryo is surrounded by a vascular plexus in which the blood performs a continuous circulatory movement. The heart is at this time a bent tube giving origin to two main arteries, the aortæ, which, after curving backward, run on each side, for nearly the whole length of the body of the embryo, beneath the protovertebræ, in the inferior lamina of the mesoderm. (Figs. 185 and 186, *ao*). Near the posterior extremity of the provertebral chain they supply two large branches, the *vitelline arteries*, which pass out, one on each side, to ramify in the area vasculosa. When first formed these arteries are of wide calibre, and their branches communicate with each other by frequent inosculations, both in the immediate neighborhood of the embryo and in the area vasculosa. The vena terminalis, after making the circuit of the area vasculosa, curves backward in front of the embryo on each side, near the median line, forming the *anterior vitelline veins*, right and left. These veins are not only supplied with blood from the vascular plexus, but also receive inosculating branches from the adjacent portions of the vena terminalis. They continue backward to a point just behind the situation of the heart, where they unite with two veins coming from the sides, the *lateral vitelline veins*, by which the blood is finally returned from the area vasculosa to the venous extremity of the heart.

The circulation of the area vasculosa transfers to the embryo the nutritious fluids of the vitellus. The blood distributed over the surface of the yolk absorbs its organic materials and returns with them by the vitelline veins; and by a continuation of this movement the nutritive substances stored up in the yolk sac are utilized for the growth of the embryonic tissues. After the establishment of this circulation, accordingly, the development of the embryo goes on with increased rapidity. The subsequent changes vary in different species and classes according to the final disposition and relative importance of various parts; but in all vertebrate animals the origin and early formation of the organs follow a similar course to that in the fowl's egg during incubation.

CHAPTER VIII.

ACCESSORY EMBRYONIC ORGANS; UMBILICAL VESICLE, AMNION, AND ALLANTOIS.

THUS far the process of development relates to the principal parts of the body of the embryo. In some species this includes all the important structures in the impregnated egg; the embryo arriving very soon at a stage of growth in which it is capable of an independent existence. But in many fish and reptiles, and in all birds and mammalia, additional structures are produced, which aid in the protection or nutrition of the embryo during the middle and later periods of its development. In these instances certain portions of the blastoderm, like those forming the area vasculosa in the fowl's egg, remain outside the body, and assume the function of accessory organs. The most important of these are the umbilical vesicle, the amnion, and the allantois.

Umbilical Vesicle.

In the frog's embryo (page 620), the abdominal plates, closing together in front, join each other upon the median line; thus shutting in the vitellus, and enclosing it in the future intestinal canal.

In other instances the abdominal plates do not immediately embrace the whole of the vitelline mass, but approach each other at some intermediate point; constricting the vitellus and dividing it by this means into two portions, one of which is included within the body of the embryo, while the other remains outside (Fig. 192). As development proceeds, and the embryo increases in size, the constriction becomes more strongly marked, forming a nearly complete separation between the internal and external portions of the vitellus. The internal portion remains as part of the intestinal canal; while the external portion, with its blastodermic covering, forms a sac-like appendage to the abdomen, attached at the umbilicus, and known as the *umbilical vesicle.*

Fig. 192.

Egg of Fish, showing formation of umbilical vesicle.

The umbilical vesicle is accordingly lined by a portion of the internal blastodermic layer, continuous with the epithelium of the intestine; and covered by a portion of the external blastodermic layer, continuous with the integument of the abdomen.

After the young animal leaves the egg, the umbilical vesicle in some species becomes shrunken and atrophied by the absorption of its contents. In others the abdominal walls gradually extend over it, and crowd it back into the abdomen; the nutritious matter which it contains passing into the intestine by the narrow passage remaining between them.

Fig. 193.

Human Embryo, with umbilical vesicle; about the fifth week.

In man, as well as in quadrupeds, the umbilical vesicle becomes more completely separated from the abdomen. There is at first a wide communication between the two; but this communication is subsequently narrowed by the gradual constriction of the abdominal walls, and the opposite surfaces of the canal at last come in contact and unite with each other. The passage is thus obliterated; and the umbilical vesicle is then connected with the abdomen only by an impervious cord. The cord afterward increases in length, becoming a slender pedicle (Fig. 193), connected at its farther extremity with the umbilical vesicle, which is filled with a transparent, colorless fluid. The umbilical vesicle of the human fœtus is distinctly visible until the end of the third month. After that period it diminishes in size, and is gradually lost in the advancing development of the neighboring parts.

Amnion and Allantois.

The amnion and allantois are closely related in their physiological importance, since the first necessarily precedes the formation of the second. The amnion is developed from the external layer of the blastoderm; the allantois from its internal layer. The amnion is so called probably from the Greek ἀμνὶς, a young lamb; from its having been first observed as a fœtal envelope in this animal. The name of the allantois is derived from the Greek ἀλλαντοειδὴς, owing to its elongated or sausage-like form in some of the domestic animals.

Both these organs are connected with the nutrition of the embryo within the egg. In birds and quadrupeds, the young animal, while still enclosed by the membranes, reaches a high grade of organization; and the processes of absorption, respiration, and exhalation necessary for its growth require a special organ for their accomplishment. This organ, which brings the blood of the fœtus into relation with external sources of nutrition, is the *allantois*.

In the frog and similar species, the internal blastodermic layer, forming the lining membrane of the intestine, is everywhere inclosed by the external layer, forming the integument. But in the higher animals a portion of the internal layer, destined to produce the allantois, is brought into contact with the external membrane of the egg for purposes of exhalation and absorption; and this can only be accomplished by opening a passage for it through the external blastodermic layer. This is done by the formation of the *amnion.*

Soon after the body of the embryo has been sketched out, mainly by the thickening of a portion of the external blastodermic layer, a secondary fold of this layer rises up on all sides about the edges of the newly-formed embryo; so that its body appears as if sunk in a kind of depression, surrounded by a membranous ridge, as in Fig. 194. The embryo (*c*) is here seen in profile, with the external folds, above mentioned, rising up in advance of the head, and behind the posterior extremity. The same thing takes place on the two sides, by the formation of lateral folds simultaneously with the appearance of those in front and behind. As these folds are destined to form the amnion, they are called the "amniotic folds."

FIG. 194.

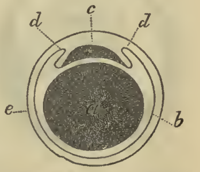


Diagram of the FECUNDATED EGG; showing the formation of the amnion.—*a.* Vitellus. *b.* External blastodermic layer. *c.* Body of the embryo. *d, d.* Amniotic folds. *e.* Vitelline membrane.

The amniotic folds continue to grow, covering the embryo and approaching each other over its dorsal region (Fig. 195). Their edges afterward come in contact and unite with each other at this point (Fig. 195, *b*), so as to shut in a space between them and the body of the embryo. This space, which contains a layer of clear fluid, is the amniotic cavity.

There now appears a prolongation or diverticulum (Fig. 195, *c*), growing from the posterior portion of the intestinal canal, and following the course of the amniotic fold which has preceded it; occupying, as it protrudes, the space thus left vacant. This diverticulum is the commencement of the allantois. It is an elongated membranous sac, continuous with the posterior portion of the intestine, and containing blood-vessels derived from those of the intestinal circulation. Its cavity communicates with that of the intestine.

FIG. 195.

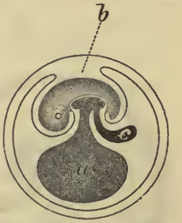


Diagram of the FECUNDATED EGG, farther advanced.—*a.* Umbilical vesicle. *b.* Amniotic cavity. *c.* Allantois.

After the amniotic folds have approached and touched each other over the back of the embryo, their adjacent surfaces fuse together at the point of contact; so that the cavities of the two folds, coming respectively from front and rear, are separated only by a single membranous partition (Fig. 196, *c*) connecting the inner and outer laminæ of the amniotic folds. This partition is afterward atrophied and disappears; and the inner and outer laminæ become separated from each other. The inner lamina (Fig. 196, *a*) remains continuous with the fœtal integument, thus enclosing the embryo in a distinct cavity. It is called the *amnion*, and its cavity is known as the amniotic cavity. The outer lamina, on the other hand (Fig. 196, *b*), comes in contact with the original vitelline membrane and fuses with its substance, so that the two form but one. This membranous layer, resulting from the consolidation of two others, then constitutes the external investing membrane of the egg.

FIG. 196.

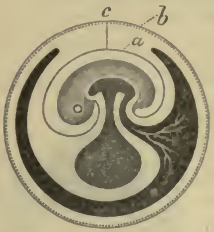


Diagram of the FECUNDATED EGG, with allantois nearly complete.—*a.* Inner lamina of amniotic fold. *b.* Outer lamina of amniotic fold. *c.* Point where the amniotic folds come in contact. The allantois is seen penetrating between the inner and outer laminæ of the amniotic folds.

The allantois, in the mean time, increases in size and vascularity. Still following the course of the amniotic folds, it insinuates itself between them, until it comes in contact with the external membrane above described. It then begins to expand laterally, growing round the body of the embryo, and bringing its vessels into contact with the external investing membrane of the egg.

By a continuation of this process the allantois completely envelops the body of the embryo; its opposite borders coming in contact and fusing with each other over the dorsal region, in the same manner as the amniotic folds had previously done (Fig. 197). It lines the whole internal surface of the investing membrane with a flattened, vascular sac; its blood-vessels coming from the interior of the body of the embryo, and its cavity still communicating with that of the intestinal canal.

It is evident, accordingly, that there is a close connection between the formation of the amnion and that of the allantois. It is by this means that the allantois, which is originally an extension of the internal blastodermic layer, comes to be situated outside the embryo and the amnion, and is brought into relation with surrounding media. The two laminæ of the amniotic folds, by separating from each other as above described, open a passage for the allantois, through which it comes in contact with the external membranous investment of the egg.

FIG. 197.

Diagram of the FECUNDATED EGG, with the allantois fully formed.—*a.* Umbilical vesicle. *b.* Amnion. *c.* Allantois.

Physiological Action of the Allantois.—The physiological action of the allantois, in its simplest character, may be studied with advantage in the fowl's egg, where it forms an extensive and highly vascular organ, without important modification of its original structure.

The egg of the fowl contains, when first laid, an abundant deposit of semi-solid albuminous matter in which the yolk is enveloped. This affords, in connection with the yolk, a sufficient quantity of moisture and organic nutriment for the growth of the embryo. The necessary warmth is supplied by the fowl in incubation; and the atmospheric gases can pass without difficulty through the porous shell and its lining membranes. On the commencement of incubation, a liquefaction takes place in the albumen above the blastoderm; allowing the vitellus to rise toward the surface by virtue of its less specific gravity, and bringing the blastoderm almost immediately beneath the lining membrane of the shell. The embryo is thus placed in a favorable position for the reception of warmth and other necessary external influences. The liquefied albumen is absorbed by the vitelline membrane, and the yolk becomes larger, softer, and more diffluent than before incubation.

In the earliest stages of the embryonic circulation the body of the embryo is surrounded, in the adjacent parts of the blastoderm, by the inosculating blood-vessels of the *area vasculosa* (page 637). As development proceeds, this area increases in extent and its circulation becomes more active. It covers the upper hemisphere of the yolk; and then, passing this level, embraces more and more of its inferior hemisphere, extending nearly to its opposite pole.

During this period the amnion and the allantois are in process of formation. At first the embryo lies upon its abdomen, as heretofore described; but, as it increases in size, it alters its position so as to lie upon its left side. The allantois, emerging from the abdominal cavity, turns upward over the body of the embryo, and comes in contact with the shell membrane. It then expands in every direction, toward the extremities and down the sides of the egg, enveloping the embryo and the vitelline sac, and taking the place of the albumen which has been liquefied and absorbed.

When the umbilical vesicle is formed, by the partial separation of the yolk from the abdomen of the embryo, the vessels of the area vasculosa, at first distributed over the yolk, then ramify upon the surface of the umbilical vesicle.

At last the allantois, by its continued growth, surrounds nearly all the remaining parts; so that, at whatever point the egg may be opened, the internal surface of the shell membrane is found to be lined with a vascular expansion. This expansion is the allantois, supplied by arteries emerging from the body of the embryo.

The allantois in the fowl's egg is accordingly adapted, by its structure and position, to perform the office of a respiratory organ. The air penetrates from without through the porous shell and its lining membranes, and acts upon the blood in the vessels of the allantois in the same way as in the pulmonary capillaries of the adult animal. Examination of the egg, at various periods of incubation, shows that it undergoes changes similar to those of respiration.

The egg, in the first place, during the development of the embryo, loses water by exhalation. This is not the result of simple evaporation, but depends upon nutritive changes in the interior of the egg; since it does not take place to the same degree in unimpregnated eggs, nor in those which are not incubated, though freely exposed to the air. It is also essential to development; since in hatching eggs by artificial warmth, if the air of the hatching chamber become charged with moisture, so as to retard or prevent further exhalation, the development of the embryo is arrested. The loss of substance during natural incubation, mainly from the exhalation of water, has been found by Baudrimont and St. Ange* to be over 15 per cent. of the entire weight of the egg.

Secondly, the egg absorbs oxygen and exhales carbonic acid. The two observers above mentioned ascertained that during eighteen days' incubation, the fowl's egg absorbs nearly two per cent. of its weight of oxygen, while the carbonic acid exhaled from the sixteenth to the nineteenth day amounts to nearly $\frac{1}{5}$ of a gramme in twenty-four hours. It is also observed that in the egg during incubation, as well as in the adult animal, more oxygen is absorbed than is returned by exhalation under the form of carbonic acid.

The allantois, however, is not simply an organ of respiration; it also takes part in the absorption of nutritious matter. As development advances, the skeleton of the chick, at first cartilaginous, begins to ossify. The calcareous matter necessary for this process is in great part derived from the shell. The shell is perceptibly lighter and more fragile toward the end of incubation than at first; and, at the same time, the mineral constituents of the embryonic skeleton increase in quantity. The lime-salts, requisite for ossification, are absorbed from the shell by the vessels of the allantois, and transferred to the bones of the chick; so that, as the former becomes weaker, the latter grow stronger. The diminution in density of the shell is connected not only with the development of the skeleton, but also with the final release of the chick from the egg. This deliverance is accomplished mainly by the chick's movements, which become, at a certain period, sufficiently vigorous to break the attenuated shell. The first fracture is generally accomplished by a stroke from the end of the bill; and it is precisely at this point that the deposit of osseous matter is most abundant. The egg-shell, therefore, which at first serves for the protection of the embryo, afterward furnishes the materials which are to accomplish its own demolition, and thus allow the escape of the fully developed chick.

Toward the end of incubation, the allantois becomes more adherent to the internal surface of the shell-membrane. At last, when the chick at its full period of development leaves the egg, the allantoic vessels are torn off at the umbilicus; and the allantois is left behind as an effete organ in the cavity of the abandoned shell.

Both the amnion and the allantois are, therefore, formations belonging to the embryo, and constituting, for a time, accessory parts of its organization. Developed from the peripheral portions of the blastoderm, they are important structures during the middle and latter periods of incubation; but when the young animal has become sufficiently developed to carry on an independent existence, they are detached from their connections, and replaced by other organs belonging to the adult condition.

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* Développement du Fœtus. Paris, 1850, p. 143.

CHAPTER IX.

MEMBRANES OF THE IMPREGNATED EGG IN THE HUMAN SPECIES. AMNION AND CHORION.

IN man, as well as in many animals, the fœtus is enveloped in two membranes, an inner and an outer, derived respectively from the external and internal blastodermic layers, and consequently parts of the embryonic organism. While the inner of these envelopes has the same characters in man as elsewhere, the outer presents such modifications of structure as to have received a distinct name. In animals, therefore, the fœtal membranes are called the amnion and the allantois; in man, they are known as the amnion and the chorion.

Amnion.

The formation of the amnion in the human species takes place in the manner already described (page 641), namely, by the growth of a circumvallation or surrounding fold of the external blastodermic layer, which extends itself in such a way that its edges meet and coalesce over the dorsal region, inclosing the embryo in a distinct cavity.

FIG. 198.

HUMAN EMBRYO AND ITS ENVELOPES, about the end of the first month.—1. Umbilical vesicle. 2. Amnion. 3. Chorion.

FIG. 199.

HUMAN EMBRYO AND ITS ENVELOPES, at the end of the third month; showing the enlargement of the amnion.

At the time of its formation, the amnion closely embraces the body of the embryo; the opposite surfaces lying nearly in contact, with hardly any space between the two. This space afterward enlarges and becomes the amniotic cavity, containing a little colorless, transparent, serous fluid, the amniotic fluid. But throughout the earlier periods of development the cavity of the amnion is small, as compared with that of the entire egg; and the space between the amnion and the external membrane, or chorion (Fig. 198), is occupied by an amorphous gelatinous material, in which the umbilical vesicle and its stem lie imbedded.

Subsequently the amnion enlarges more rapidly, in comparison with the remaining parts of the egg, and thus encroaches upon the layer of gelatinous material by which it is surrounded. At the same time the amniotic fluid increases in quantity (Fig. 199); so that a considerable space is left around the embryo, in which it is supported by the uniform pressure of the amniotic fluid. The amnion continues to enlarge at this increased rate until about the beginning of the fifth month, when it comes in contact with the inner surface of the chorion; the intervening gelatinous material having by that time disappeared, or being reduced to a nearly imperceptible layer.

Chorion.

The chorion, in the human species, is the external enveloping membrane of the embryo. It originates, like the allantois in the lower animals, by an outgrowth from the posterior portion of the alimentary canal, which, insinuating itself between the laminæ of the amniotic folds, spreads over and around the amnion, so as to occupy finally a position outside of it. It there meets with the two thin layers which have preceded it, namely, the outer lamina of the amniotic fold, and the original vitelline membrane. But these layers, ceasing to grow, while the new structures of the egg are rapidly enlarging, disappear as distinct membranes, and are replaced by the chorion, which thus becomes the external investment of the egg.

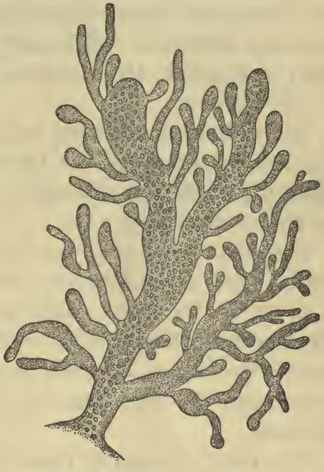
So far, the development of the chorion is similar to that of the allantois. But its distinguishing peculiarity is that, while extending over and around the other parts, it does not present the form of a sac containing fluid, but that of a vascular sheet or membrane, like the skin. On this account it is called the *chorion*, while in the lower animals it retains the name of allantois.

Nevertheless, at its commencement, the chorion is, like the allantois, a hollow membranous sac, the cavity of which is continuous with that of the intestine. But this cavity extends only a short distance outside the body of the embryo. Beyond this point its walls remain in contact with each other, forming a single membrane. Inside the body of the embryo, on the other hand, it retains the sac-like form; and this portion afterward becomes the urinary bladder. The rounded cord or "urachus," which, in the adult, runs from the superior fundus of the bladder to the umbilicus, is the vestige of the obliterated canal of the primitive chorion.

The next peculiarity of the chorion is, that *it becomes shaggy.* Even while the egg is still very small, and has but recently found its way into the uterus, its exterior is covered with villi (Fig. 198), which increase its extent of surface, and assist in the absorption of fluids from without. The villi are at this time simple in form, and homogeneous in structure.

As the egg increases in size, the villi elongate, and become ramified by the repeated budding of lateral offshoots. After this process has continued for some time, the chorion presents a uniformly shaggy appearance, owing to the abundant compound villosities which cover its surface.

Fig. 200.



Compound Villosity of the Human Chorion, ramified extremity. From a three months' fœtus. Magnified 30 diameters.

These villosities, when examined by the microscope, have an exceedingly characteristic appearance. They originate from the chorion by a somewhat narrow stem, and divide into secondary and tertiary branches of varying size and figure; some filamentous, others club-shaped, many irregularly swollen at various points. All terminate by rounded extremities, giving to the whole tuft a resemblance to some varieties of sea-weed. The larger trunks and branches of the villosity contain minute nuclei, imbedded in a nearly homogeneous, or finely granular substratum. The smaller ramifications appear, under a low magnifying power, simply granular in texture.

Fig. 201.

Extremity of a Villosity of the Chorion, magnified 180 diameters; showing the blood-vessels in its interior.

The villi of the chorion are different from any other structure in the body. Whenever any portion of a membrane with villosities of this character is discharged from, or is found in, the cavity of the uterus, it is certain that pregnancy has existed; for such villosities can only belong to the chorion, and the chorion is a part of the fœtus. The presence of a shaggy chorion is therefore as satisfactory proof of the existence of pregnancy, as if the body of the fœtus itself had been found.

While the villosities just described are in process of formation, the chorion receives a supply of blood-vessels from the body of the embryo. The arteries, which are a continuation of those distributed to the intestine, pass out along the canal of communication to the chorion and ramify over its surface. The embryo at this time has reached such an activity of growth that it requires to be supplied with nourishment by means of vascular absorption, instead of the slow process of imbibition hitherto taking place through the villi of the chorion. The capillary blood-vessels, with which the chorion is supplied, penetrate its villosities. They enter the base of each villus, and following the division of its compound ramifications, reach the extremities of its terminal offshoots. Here they turn upon themselves in loops (Fig. 201), and retrace their course, to unite finally with the venous trunks of the chorion.

The villi of the chorion are, accordingly, analogous in structure and function to those of the intestine; their power of absorption corresponding with the abundance of their ramifications, and the extent of their vascularity.

The blood-vessels of the chorion, furthermore, are derived from the fœtus; and all substances absorbed by them are transported to the interior of the body, and used for the nourishment of its tissues. The chorion, therefore, as soon as its villi and blood-vessels are completely developed, becomes an essential organ for the nutrition of the fœtus, and the only means by which new material is introduced from without.

The third change of importance in the chorion is that after being at first shaggy throughout, it *becomes partially bald.* (Fig. 199.) This change begins about the end of the second month, commencing at the point farthest from the insertion of the fœtal blood-vessels. The villosities of this region cease growing; and while the entire chorion continues to enlarge, they fail to keep pace with its progressive expansion. They accordingly become at this part thinner and more scattered, leaving the surface comparatively bald. This baldness increases in extent, spreading over the adjacent portions of the chorion, until at least two-thirds of its surface have become nearly or quite clear of villosities.

At the opposite pole of the egg, namely, that which corresponds with the insertion of the fœtal blood-vessels, the villosities of the chorion, instead of becoming atrophied, continue to grow; and this portion becomes even more shaggy and thickly set than before. The consequence is that the chorion afterward presents a different appearance in different regions. The greater part is smooth; but a certain portion, constituting about one-third of the whole, is covered with long, thickly-set, compound villosities. It is this thickened portion which is concerned in the formation of the *placenta;* while the remainder continues to be known under the name of the chorion. The placental portion of the chorion becomes distinctly limited in outline by about the end of the third month.

The vascularity of the chorion keeps pace, in its different parts, with the development of its villosities. As the villosities shrivel and disappear over a part of its extent, the blood-vessels with which they were supplied diminish in abundance; and the smooth portion of the chorion finally shows only a few straggling vessels running over its surface, without any abundant capillary plexus. In the thickened portion, on the other hand, the blood-vessels lengthen and ramify to an extent corresponding with that of the villosities in which they are situated. The arteries, coming from the fœtus, divide into branches which penetrate the villi throughout; forming, at the placental portion of the chorion, a mass of tufted and ramified vascular loops, while in the rest of the membrane the vascular supply is comparatively scanty.

The chorion, accordingly, is the external investing membrane of the egg, produced by an outgrowth from the body of the embryo; and the placenta, so far as it consists of the fœtal membranes, is a part of the chorion, distinguished by the local development of its villi and blood-vessels.

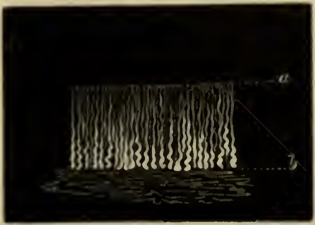
CHAPTER X.

DEVELOPMENT OF THE DECIDUA, AND ATTACHMENT OF THE FŒTAL MEMBRANES TO THE UTERUS.

IN the human species, where the embryo is developed within the uterus, it depends for its nutrition upon materials derived from the female parent. The immediate source of this supply is the mucous membrane of the uterus, which becomes unusually developed during gestation, and, when thus modified in structure, is known as the *decidua.* It has received this name from the fact that it is thrown off and discharged at the same time that the fœtus and its membranes are expelled from the uterus.

The mucous membrane of the body of the uterus, in the unimpregnated condition, presents a smooth internal surface. There is no distinct layer of connective tissue between it and the muscular substance beneath; so that the mucous membrane cannot here, as in most other organs, be readily separated by dissection from the subjacent parts. Its structure, however, is well marked. It consists, throughout, of tubular follicles, arranged side by side, perpendicularly to its free surface. Near this surface they are nearly straight; but toward the deeper part of the membrane, where they terminate in blind extremities, they become more or less wavy or spiral in their course. They are about 0.05 millimetre in diameter, and are lined with columnar epithelium. They occupy the entire thickness of the

FIG. 202.



UTERINE MUCOUS MEMBRANE, from the unimpregnated uterus, in vertical section. *a.* Free surface. *b.* Attached surface. Magnified about 10 diameters.

FIG. 203.

UTERINE TUBULES, from the mucous membrane of an unimpregnated human uterus. Magnified 125 diameters.

mucous membrane, their closed extremities resting on the subjacent muscular tissue, while their mouths open into the cavity of the uterus. A few fine blood-vessels penetrate the mucous membrane from below, and, running upward between the tubules, encircle their superficial extremities with a capillary network. There is no connective tissue in the uterine mucous membrane, but only a few isolated nuclei and spindle-shaped fibre-cells between the tubules.

Decidua Vera.—As the fecundated egg descends through the Fallopian tube, the uterine mucous membrane takes on an increased activity of growth. It becomes tumefied and vascular; and, as it increases in thickness, it projects, in rounded eminences, into the uterine cavity. (Fig. 204.) The uterine tubules increase both in length and in width; and their open mouths become perceptible on the uterine surface, like minute perforations. According to Kölliker, so early as the end of the first week, they have increased to three or four times their original size, measuring on the average 0.20 millimetre in diameter. The blood-vessels of the mucous membrane also enlarge and communicate freely with each other; the vascular network between and around the tubules thus becoming more extensive and abundant. The internal surface of the uterus presents a thick, rich, soft, velvety, and vascular lining, quite different from that found in the unimpregnated condition. It is now known as the decidua; and, in order to distinguish it from a similar growth of subsequent formation, it has received the special name of the *decidua vera.*

The production of the decidua is confined to the body of the uterus, the mucous membrane of the cervix taking no part in the process, but retaining its original appearance. The decidual membrane commences above, at the orifices of the Fallopian tubes, and ceases below, at the os internum. The cavity of the cervix, meanwhile, is filled with an abundant secretion of viscid mucus, which blocks up its passage, and protects the internal cavity. If the uterus be opened in this condition, its body will be seen lined with the decidua vera, which is continuous, at the os internum, with the unaltered mucous membrane of the cervix.

Decidua Reflexa.—As the fecundated egg passes the lower orifice of the Fallopian tube, it insinuates itself between the opposite surfaces of the uterine mucous membrane, and becomes lodged in one of the depressions between the folds of the decidua. (Fig. 204.) At this situation an adhesion subsequently takes place between the external membrane of the egg and the uterine decidua. At the point where the egg thus becomes fixed, there is a still more rapid development of the uterine mucous membrane. Its projecting folds grow up around the egg in such a manner as to partially enclose it in a kind of circumvallation, and shut it off, in great measure, from the surrounding parts. (Fig. 205.) The egg thus comes to be contained in a cavity of its own, which still communicates for a time with the general cavity of the uterus, by an opening over its most prominent part. As the process goes on, this opening becomes narrower, while the decidual folds approach each other over the surface of the egg. At last they come in contact and unite with each other, forming a kind of cicatrix, which remains for a time, to mark the situation of the original opening.

When the development of the uterus has reached this point (Fig. 206), the egg is completely enclosed; being covered with a decidual layer of new formation, by which it is concealed from view when the uterine cavity is laid open. This newly-formed layer, enveloping the projecting portion of the egg, is called the *Decidua reflexa;* because it is reflected over the egg from the general surface of the uterine mucous membrane. The orifices of the uterine tubules, in consequence of the manner in which the decidua reflexa is formed, are seen not only on its external surface, or that which looks toward the cavity of the uterus, but also on its internal surface, or that which looks toward the egg.

Fig. 204.

Impregnated Uterus; showing formation of decidua. The decidua is represented in black; and the egg is seen, at the fundus of the uterus, engaged between two of its projecting folds.

Fig. 205.

Impregnated Uterus, with folds of decidua growing up around the egg. The narrow opening, where the folds approach each other, is seen over the most prominent portion of the egg.

Fig. 206.

Impregnated Uterus; showing the egg completely enclosed by the decidua reflexa.

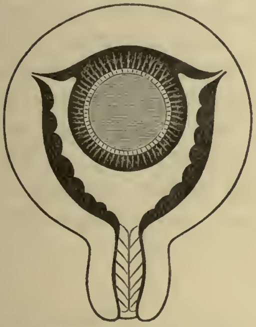
The decidua vera, therefore, is the original mucous membrane of the uterus. The decidua reflexa is a new formation, which grows up around the egg, to enclose it in a distinct cavity.

If abortion occur at this time, the mucous membrane of the uterus, that is, the decidua vera, is thrown off, and brings with it the egg and the decidua reflexa. On examining the mass so discharged, the egg will be found imbedded in the decidual membrane. One side of the membrane, where it has been torn away from the uterus, is ragged; the other side, corresponding to the uterine cavity, is smooth or gently convoluted, and exhibits distinctly the orifices of the uterine tubules; while the egg itself can only be extracted by cutting through the decidual membrane, either from one side or the other, and opening in this way the special cavity in which it is enclosed.

During the formation of the decidua reflexa, the entire egg, as well as the body of the uterus, has considerably enlarged. That portion of the uterine mucous membrane situated immediately beneath the egg, and to which it first became attached, has also become thicker and more vascular. The remainder of the decidua vera, however, no longer keeps pace with the increasing size of the egg and of the uterus. It is still thick and vascular at the end of the third month; but after that period it becomes thinner and less consistent, while the principal activity of growth is concentrated in that portion of the uterine mucous membrane which is in immediate contact with the egg.

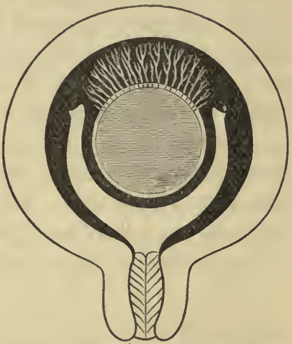
Attachment of the Fœtal Membranes to the Uterus.—While the above changes are taking place in the uterus, the formation of the embryo, and the development of its membranes have been going on simultaneously; and soon after the entrance of the egg into the uterine cavity, the chorion is covered with villosities which insinuate themselves into the uterine tubules, or between the folds of the decidua. When the formation of the decidua reflexa is complete, the chorion has become uniformly shaggy; and its villosities penetrate both into the decidua vera beneath it and into the decidua reflexa with which it is covered. In this way it becomes everywhere entangled with the decidua, and cannot be readily separated without rupturing some of the filaments which have grown from its surface into the substance of the decidua. The nutritious fluids, exuded from the decidua, are now imbibed by the villosities of the chorion; and a more rapid supply of nourishment is thus provided, corresponding with the greater size of the egg.

FIG. 207.



IMPREGNATED UTERUS; showing the connection between the villosities of the chorion and the decidual membranes.

FIG. 208.



PREGNANT UTERUS; showing the formation of the placenta by the local development of the decidua and the chorion.

Very soon the activity of absorption is still further increased. The chorion becomes vascular, by the formation of blood-vessels emerging from the embryo and penetrating the villosities with which it is covered.

Each villosity then contains a vascular loop, imbedded in its substance, and serving to absorb from the decidua the materials for the growth of the embryo.

Subsequently, the vascular tufts of the chorion, at first uniformly distributed over its surface, disappear from the greater part of its extent, becoming more highly developed at a particular point, the situation of the future placenta. This is the spot at which the egg is in contact with the decidua vera. Here, both the decidual membrane and the tufts of the chorion continue to increase in thickness and vascularity while elsewhere, over the prominent portion of the egg, the chorion not only becomes bare of villosities and comparatively destitute of blood-vessels, but the decidua reflexa, in contact with it, also loses its activity of growth and becomes expanded into a thin layer, without any remaining trace of glandular follicles.

The uterine mucous membrane is therefore developed, during gestation, in such a way as to provide for the nourishment of the embryo in the different stages of its growth. At first, the whole of it is uniformly increased in thickness (decidua vera). Next, a portion of it grows upward around the egg, and covers its projecting surface (decidua reflexa). Afterward, both the decidua reflexa and the greater part of the decidua vera diminish in the activity of their growth, and lose their importance as a means of nourishment for the embryo; while that part which is in contact with the vascular tufts of the chorion continues to grow, becoming excessively developed, and taking part in the formation of the placenta.

CHAPTER XI.

THE PLACENTA.

IN man and mammalians the embryo, during intra-uterine life, is dependent upon the uterus for the materials of its growth; and this supply of nourishment is provided by means of two vascular membranes. One of these membranes, the chorion or allantois, is an outgrowth from the embryo; the other is the mucous membrane of the uterus. By their more or less intimate juxtaposition, the fluids transuded from the blood-vessels of the mother are absorbed by those of the embryo, and a transfer of nutriment thus takes place from the maternal to the fœtal organism.

In some animals, the connection between the maternal and fœtal membranes is a simple one. In the pig, the uterine mucous membrane is everywhere uniformly vascular; its only peculiarity consisting in the presence of transverse folds, projecting from its surface, like the valvulæ conniventes of the small intestine. The surface of the allantois is also smooth and uniformly vascular. No special development occurs at any part of these membranes, and no adhesion takes place between them. The vascular allantois of the fœtus lies in simple apposition with the vascular mucous membrane of the uterus, each of the contiguous surfaces following the undulations of the other; and the transudation and absorption between the two sets of blood-vessels provide for the nutrition of the fœtus. When parturition takes place, a moderate contraction of the uterus is sufficient to expel its contents; the egg being displaced from its position and discharged from the uterus without hemorrhage or laceration of the parts.

In other instances, there is a more intimate connection, at certain points, between the fœtal and maternal structures. In the cow, sheep, and ruminating animals generally, the external membrane of the egg, beside being everywhere supplied with blood-vessels, presents, scattered over its surface, numerous rounded or oval spots, covered with thickly set, tufted, vascular prominences. These spots are called *cotyledons*, or cups, because each one is surrounded by a rim or fold, which embraces a corresponding mass projecting from the inner surface of the uterus. This portion of the uterine mucous membrane is also abundantly supplied with blood-vessels; and the vascular tufts of the fœtal membrane are entangled with those belonging to the uterus. There is no absolute adhesion between the two sets of vessels, but only an interlacement of their ramified extremities; and by careful manipulation the fœtal portion, with its villosities, may be extricated from the maternal portion without the laceration of either.

In the carnivorous animals, a similar highly developed, vascular portion of the allantois runs, in the form of a broad belt, round its middle; corresponding in situation with an equally developed zone of the uterine mucous membrane. Here the fœtal and maternal structures are mutually adherent; while, elsewhere, over both extremities of the egg, they lie simply in contact with each other. When gestation comes to an end, and the fœtus, with its membranes, is expelled, the thickened zone of uterine mucous membrane is detached at the same time, its place being afterward made good by a new growth.

In man, as shown in the preceding chapter, the permanently thickened portions of the chorion and decidua are united with each other, by mutual interpenetration, in a flattened, cake-like mass of rounded form, occupying rather less than one-third of the surface of the chorion, and corresponding to a similar extent of the inner surface of the uterus. This mass, consisting of the fœtal and maternal elements combined, is the *placenta.*

The development of the placenta takes place in the following manner:

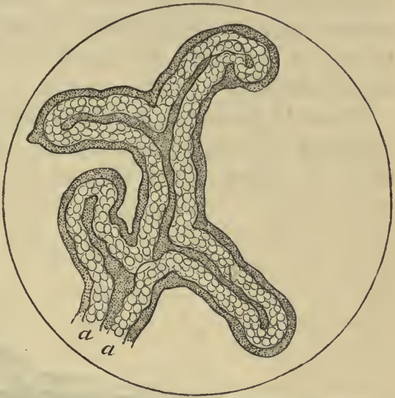
The villi of the chorion, when first formed, penetrate the follicles of the uterine mucous membrane; and are afterward developed into tufted vascular ramifications, each of which turns upon itself in a loop at the farther extremity of the villus. At the same time the uterine follicle, into which the villus has penetrated, enlarges to a similar extent; sending out branching diverticula, corresponding with the ramifications of the villus. The growth of the follicle and that of the villus thus go on simultaneously and keep pace with each other; the latter constantly advancing as the former enlarges.

But it is not only the uterine follicles which increase in size and in complication of structure. The capillary blood-vessels between them also become unusually developed by enlargement of their inosculations; so that every follicle is covered with a network of dilated capillaries, derived from the blood-vessels of the original decidua.

As the formation of the placenta goes on, the arrangement of the fœtal blood-vessels remains the same. They continue to form vascular loops, penetrating deeply into the decidual membrane; only they become more elongated, and their ramifications more abundant and tortuous. The maternal capillaries, however, on the outside of the uterine follicles, are considerably altered in their anatomical relations. They enlarge in all directions, and, encroaching upon the spaces between them, fuse successively with each other; losing in this way the form of a capillary network, and becoming dilated into sinuses, which communicate freely with those in the walls of the uterus. As the original capillary plexus occupied the entire thickness of the hypertrophied decidua, the vascular sinuses, into which it is thus converted, are equally extensive. They commence at the uterine surface of the placenta, where it is in contact with the muscular walls of the organ, and extend through its whole thickness, to the outer surface of the fœtal chorion.

As the maternal sinuses grow inward, the vascular tufts of the chorion grow outward, through all parts of the placenta. In the latter periods of pregnancy, the development of blood-vessels, both fœtal and maternal, in the placenta, is so excessive that all the other tissues, which originally coexisted with them, have nearly disappeared. If a villus from the fœtal portion of the placenta be examined at this time in the fresh condition (Fig. 209), it will be seen that its blood-vessels are covered only with a homogeneous or finely granular layer, about 7 mmm. in thickness, in which are imbedded small oval nuclei, similar to those at an earlier period in the villosities of the chorion. The placental villus is now hardly anything more than a congeries of tortuous vascular loops; its remaining substance having been absorbed in the excessive growth of the blood-vessels, the abundance and development of which can be shown by injection from the umbilical arteries. (Fig. 210.) The uterine follicles have lost their original structure, and have become vascular sinuses, surrounding the tufts of fœtal blood-vessels.

Fig. 209.



Extremity of a Fœtal Tuft, from the placenta at term, in its recent condition.—*a. a.* Capillary blood-vessels. Magnified 135 diameters.

Fig. 210.

Extremity of a Fœtal Tuft of the placenta; from an injected specimen. Magnified 40 diameters.

Finally, the walls of the fœtal blood-vessels having come into close apposition with those of the maternal sinuses, the two become adherent and fuse together; so that at last the fœtal vessels in the placenta can no longer be separated from the maternal sinuses, without lacerating either the one or the other.

The placenta, therefore, when perfectly formed, has the structure shown in the accompanying diagram (Fig. 211), which represents a vertical section through its entire thickness. At *a*, *a* is the chorion, receiving the umbilical vessels from the fœtus through the umbilical cord, and sending out its ramified vascular tufts into the placenta. At *b*, *b* is the attached surface of the decidua; and at *c*, *c*, *c*, *c* are the orifices of uterine vessels which penetrate it from below. These vessels enter the placenta in an extremely oblique direction, though they are represented in the diagram, for the sake of distinctness, as nearly perpendicular. Immediately after penetrating the decidua, they dilate into the placental sinuses (represented in the diagram in black), which extend through the whole thickness of the organ, embracing the ramifications of the fœtal tufts. At this stage of completion the placenta is essentially a vascular tissue. The other structures which originally entered into its composition have disappeared, leaving only the blood-vessels of the fœtus entangled with and adherent to the blood-vessels of the mother.

There is, however, no direct communication between the fœtal and maternal vessels. The blood of the fœtus is everywhere separated from the blood of the mother by a thin partition, resulting from the fusion of four different membranes, namely, first, the membrane of the fœtal villus; secondly, that of the uterine follicle; thirdly, the wall of the fœtal blood-vessel; and fourthly, the wall of the uterine sinus. But this partition is of great extent, owing to the abundant ramification of the fœtal vessels. The vascular tufts, in which the blood of the fœtus circulates, are everywhere bathed, in the placental sinuses, with the blood of the mother; and the interchange of material between the two, by absorption and exhalation, goes on with corresponding activity.

Fig. 211.

Vertical Section of the Placenta, showing the arrangement of the maternal and fœtal blood-vessels.—*a*, *a*. Chorion. *b*, *b*. Decidua. *c*, *c*, *c*, *c*. Orifices of uterine sinuses.

It is easy to demonstrate the arrangement of the fœtal tufts in the placenta. They can be seen by the naked eye, and may be readily traced from their attachment at the chorion to their termination near the uterine surface of the placenta. The anatomical disposition of the placental sinuses is more difficult of examination. During life, while the placenta is attached to the uterus, they are filled with the blood of the mother, occupying nearly or quite one-half the mass of the placenta.

But when the placenta is detached, and its maternal vessels torn off at their necks (Fig. 211, *c*, *c*, *c*, *c*), the sinuses, emptied of blood by the compression to which they are subjected, are apparently obliterated; and the fœtal tufts, lying in contact with each other, appear to constitute the whole of the placental mass. The existence of the sinuses, however, and their extent, may be demonstrated in the following manner:

If the uterus of a woman who has died undelivered at the full term or thereabout, be opened without wounding the placenta, this organ will be seen attached to the uterine surface, with its vascular connections complete. Let the fœtus be removed by dividing the umbilical cord, and the uterus, with the placenta attached, placed under water, with its internal surface uppermost. If a blowpipe be now inserted into one of the divided vessels of the uterine walls, and air forced through it under gentle and steady pressure, it will inflate, first, the vascular sinuses of the uterus; next, the deeper portions of the placenta; and lastly, the air-bubbles insinuate themselves everywhere between the fœtal tufts, and appear in the most superficial portions of the placenta, immediately beneath the chorion (*a*, *a*, Fig. 211). This shows that the placental sinuses, which communicate with the uterine vessels, occupy the entire thickness of the placenta, and are equally extensive with the tufts of the chorion.

If the placenta be detached and separately examined, it will be found to present on its uterine surface a number of openings, extremely oblique in position, and bounded on one side by a thin crescentic edge. These are the orifices of the uterine blood-vessels, passing into the placenta and torn off at their necks, as above described; and, by careful dissection, they are found to lead into extensive collapsed cavities (the placental sinuses), between the fœtal tufts. These cavities are filled during life with the maternal blood; and there is every reason to believe that before delivery, while the circulation is going on, the placenta is at least twice as large as after it has been expelled from the uterus.

The part taken by the placenta in the development of the fœtus is of primary importance. From the date of its formation, about the beginning of the fourth month, it is the only channel for the conveyance of nourishment from the mother to the fœtus. The nutritious materials, circulating in the maternal sinuses, pass through the intervening membrane, and enter the blood of the fœtus. The healthy or injurious regimen to which the mother is subjected will, accordingly, exert an influence upon the child. Even medicinal substances taken by the mother, and absorbed into her circulation, may transude through the placental vessels, and thus produce their specific effect on the fœtal organization.

The placenta is an organ of exhalation as well as of absorption. The excrementitious matters in the blood of the fœtus are undoubtedly disposed of in great measure by transudation through the placental vessels, to be afterward discharged by the excretory organs of the mother. The mother may therefore be affected by influences derived from the fœtus. It has been observed in animals, that when the female has two successive litters of young by different males, the young of the second litter will sometimes bear marks resembling those of the first male. In these instances, the influence which produces the mark is transmitted by the first male to the fœtus, from the fœtus to the mother, and from the mother to the fœtus of the second litter.

It is probably through the placental circulation that shocks or injuries inflicted on the mother produce disturbances in the nutrition of the fœtus. There is little room for doubt that various deformities and deficiencies of the fœtus, conformably to the popular belief, may originate from nervous impressions experienced by the mother. The mode in which these influences are conveyed is not always easy of explanation. But it is well known that nervous impressions in the adult will often cause local derangement of the circulation, through the vasomotor system, in the brain, the lungs, or the skin. The uterine circulation is peculiarly susceptible to similar influences, as shown in cases of amenorrhœa and menorrhagia. If a nervous shock to the mother may excite premature contraction in a pregnant uterus and consequent abortion, it is undoubtedly capable of causing partial or temporary disturbances of its vascularity. But the fœtal circulation is dependent, in great measure, on the maternal; and, as the nutrition of the fœtus is provided for by the placenta, it will suffer from derangement of the placental circulation. These effects may be manifested either in the general atrophy and death of the fœtus, or in the imperfect development of particular parts; as in the adult a morbid action may either operate on the entire system, or be limited to some organ especially sensitive to its influence.

CHAPTER XII.

DISCHARGE OF THE FŒTUS AND PLACENTA. REGENERATION OF THE UTERINE TISSUES.

DURING the growth of the embryo, and the development of the placenta, the muscular tissue of the uterus increases in thickness, while the whole organ enlarges, to accommodate the greater volume of its contents. This unusual growth of the muscular tissue gives it an increased contractile power sufficient for the expulsion of the fœtus at the time of delivery.

The enlargement of the amniotic cavity, and the greater abundance of the amniotic fluid, provide space for the intra-uterine movements of the fœtus. These movements begin to be perceptible about the fifth month, at which time the muscular system is sufficiently developed to show a certain amount of activity. During the latter months of pregnancy they become more frequent and vigorous, and may often be felt by the hand of the observer applied over the region of the uterus.

The attachment of the embryo to the investing membrane of the egg is at first by a short and wide funnel-shaped connection, consisting of the commencement of the chorion, a part of the amnion, and a deposit of gelatinous material between the two, containing the stem of the umbilical vesicle. Subsequently, as the amniotic cavity enlarges, the body of the embryo recedes from the inner surface of the chorion, by the elongation of its connecting part; and this part consequently begins to present the appearance of a cord (Fig. 212). It is still surrounded with a thick layer of gelatinous matter, by which it is separated from its amniotic investment. As it emerges from the embryo, at a point where the abdominal walls will afterward close round it, to form the umbilicus, it is known by the name of the *umbilical cord*. It contains the blood-vessels passing out to the chorion and placenta.

FIG. 212.

HUMAN EMBRYO AND ITS MEMBRANES, in the early period of gestation; showing the formation of the umbilical cord.

After the third month the umbilical cord and its blood-vessels elongate more rapidly than is required by the increased size of the amniotic cavity. They consequently become twisted, the two umbilical arteries winding round the vein in a spiral direction.

The direction of the spiral is not always the same. Prof. McLane has recorded observations in regard to this point upon 260 umbilical cords at term, partly in private practice and partly at the Nursery and Child's Hospital, New York. Of this number, in 138 cases the direction of the spiral was from left to right; in 112 cases, from right to left; and in the 10 remaining instances it was doubtful, the twist being too imperfectly marked for decision. This gives nearly the following percentage as the result of all the observations:

DIRECTION OF THE TWIST OF THE HUMAN UMBILICAL CORD.

From left to right	53	per cent.
From right to left	43	"
Indeterminate	4	"
	100	

There is, accordingly, no great preponderance in frequency of the twist in either direction. Two cases of twins are included in the above list; in the first of which both umbilical cords turned from right to left; in the second, one of them turned from right to left, the other from left to right. In two instances, the cord presented turns in opposite directions in different parts of its length.

FIG. 213.

PREGNANT HUMAN UTERUS AND ITS CONTENTS, about the end of the seventh month; showing the relations of the cord, placenta, and membranes.—1. Decidua vera. 2. Decidua reflexa. 3. Chorion. 4. Amnion.

The gelatinous matter deposited between the amnion and chorion gradually disappears over the greater part of these membranes, but accumulates in the umbilical cord in considerable quantity, surrounding the vessels with an elastic envelope, which protects them from injury. It is covered by an extension of the amnion, which is continuous with the integument of the abdomen, and invests the cord with an uninterrupted sheath throughout its length.

The cord also contains the stem of the umbilical vesicle. The situation of this vesicle is always between the chorion and the amnion. Its pedicle gradually elongates with the growth of the umbilical cord; and the vesicle, which generally disappears soon after the third month, sometimes remains as late as the fifth, sixth, or seventh. According to Mayer, it may even be found, by careful search, at the termination of pregnancy. When present in the middle and latter periods of gestation, it is a small, flattened sac, situated beneath the amnion, on the free surface of the placenta, at a variable distance from the insertion of the umbilical cord. A minute blood-vessel is often seen running to it from the cord, and ramifying upon its surface.

The decidua reflexa, during the latter months of pregnancy, is distended by the increasing size of the egg, and pressed against the opposite surface of the decidua vera. By the end of the seventh month, the decidua vera and decidua reflexa are in contact, though still distinct and capable of being easily separated. After that time, they become confounded with each other, forming at last a thin, friable, semi-opaque layer, in which no glandular structure is perceptible.

This is the condition of things at the termination of pregnancy. Then, the time for parturition having arrived, the hypertrophied muscular walls of the uterus contract upon its contents, expelling the fœtus, together with its membranes and the decidua.

In the human species, as well as in most quadrupeds, the membranes are usually ruptured during parturition; and the fœtus escapes first, the placenta and appendages following a few moments afterward. Occasionally the egg is discharged entire, the fœtus being afterward liberated by the laceration of the membranes. In each case the mode of expulsion is essentially the same.

The process of parturition consists in a separation of the decidual membrane, which, on being discharged, brings away the ovum with it. The greater part of the decidua vera, having fallen into a state of atrophy during the latter months of pregnancy, is by this time nearly destitute of blood-vessels, and separates without perceptible hemorrhage. The portion forming the placenta is, on the contrary, excessively vascular; and when this organ is separated, and its maternal vessels torn off at their insertion, a gush of blood takes place, accompanying or immediately following the birth of the fœtus. This normal hemorrhage, at the time of parturition, does not come directly from the uterine vessels. It consists of the blood contained in the placental sinuses, and expelled from the placenta under the pressure of the uterus. Since the blood thus lost was previously employed in the placental circulation, and since the placenta is itself thrown off at the same time, no unpleasant effect is produced by such a hemorrhage, because the quantity of blood in the rest of the vascular system remains the same. In normal parturition the lacerated uterine blood-vessels are immediately closed, after separation of the placenta, by the contraction of the muscular fibres through which they pass in an oblique direction. Hemorrhage in delivery becomes injurious only when it goes on after separation of the placenta; in which case it is supplied by the mouths of the uterine blood-vessels, left open by failure of the uterine contractions. So long as the uterus remains relaxed, the hemorrhage necessarily continues; but it is at once arrested by contraction of the uterine walls.

Regeneration of the Uterus after Delivery.—Both the mucous membrane and the muscular fibres of the uterus are replaced after delivery by tissues of new formation. The decidua is discharged at parturition; and the hypertrophied muscular tissue, after serving for the expulsion of the fœtus, undergoes a process of retrogression and atrophy.

A remarkable phenomenon connected with the renovation of the uterine tissues, is the appearance in the uterus, during pregnancy, of a new mucous membrane, underneath the old, and destined to take the place of the latter after its discharge.

If the uterus be examined immediately after parturition, it will be seen that at the spot where the placenta was attached, every trace of mucous membrane has disappeared. The muscular fibres in this situation are exposed; and the mouths of the ruptured uterine sinuses are also visible, their thin edges hanging into the cavity of the uterus, and their orifices plugged with bloody coagula.

Over the rest of the uterine surface the decidua vera has also disappeared. Here, however, notwithstanding the loss of the original mucous membrane, the muscular fibres are covered with a semi-transparent film, of whitish color and soft consistency. This film is an imperfect mucous membrane of new formation, which begins to be produced, underneath the decidua vera, as early as the beginning of the eighth month. The old mucous membrane, or decidua vera, is at this time somewhat opaque, and of a slightly yellowish color, from partial fatty degeneration. It is easily separable from the subjacent parts, owing to the atrophy of its vascular connections; and the new mucous membrane beneath it is distinguishable by its fresh color and semi-transparent aspect.

Fig. 214.

Muscular Fibres of the Unimpregnated Human Uterus; from a woman aged 40, dead of phthisis.

The mucous membrane of the cervix uteri, which takes no part in the formation of the decidua, is not thrown off in parturition. After delivery it may be seen to terminate at the os internum by a lacerated edge, where it was formerly continuous with the decidua vera.

Subsequently, a regeneration of the mucous membrane takes place over the whole extent of the body of the uterus. The membrane of new formation, already in existence at the time of delivery, becomes thicker and more vascular; and glandular tubules are gradually developed in its substance. At the end of two months after delivery, according to Longet* and Heschl,† it has regained the normal structure of uterine mucous membrane. It unites at the os internum with the mucous membrane of the cervix, and the traces of laceration at this spot afterward cease to be visible. At the point where the placenta was attached, the regeneration of the mucous membrane is less rapid; and a cicatrix-like spot is often visible at this situation for several months after delivery.

FIG. 215.

MUSCULAR FIBRES OF THE HUMAN UTERUS, ten days after parturition; from a woman dead of puerperal fever.

The first change in the muscular tissue of the uterus after delivery consists in a fatty degeneration. The muscular fibres of the unimpregnated uterus are pale, flattened, spindle-shaped bodies (Fig. 214), homogeneous or faintly granular in appearance, and measuring about 50 mmm. in length. During gestation they increase considerably in size. Their texture becomes more granular and their outlines more distinct. An oval nucleus also shows itself in the central part of each fibre. The walls of the uterus, at the time of delivery, are mainly composed of these fibres, arranged in circular, oblique, and longitudinal bundles.

FIG. 216.

MUSCULAR FIBRES OF THE HUMAN UTERUS, three weeks after parturition; from a woman dead of peritonitis.

About the end of the first week after delivery, they begin to undergo a fatty degeneration. (Fig. 215.) Their granules become larger and more prominent, soon assuming the appearance of fat granules, imbedded in the substance of the fibre. The deposit increases in abundance, and the granules continue to enlarge until they become converted into fully formed fat globules, which fill the interior of the fibre more or less completely, and mask, to some extent, its anatomical characters. (Fig. 216.) The fatty degeneration,

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* Traité de Physiologie. Paris, 1850, Génération, p. 173.

† Zeitschrift der k. k. Gesellschaft der Aerzte, in Wien, 1852.

thus induced, gives to the uterus a softer consistency, and a pale yellowish color, characteristic of this period. The altered muscular fibres are gradually absorbed, giving place to others of new formation, which already begin to show themselves before the old ones have disappeared. The process finally results in complete renovation of the muscular substance of the uterus. The organ becomes again reduced in size, compact in texture, and of a pale ruddy hue, as in the unimpregnated condition. The reconstruction of the uterine tissues is complete, according to Heschl, about the end of the second month after delivery.

CHAPTER XIII.

DEVELOPMENT OF THE NERVOUS SYSTEM, ORGANS OF SENSE, SKELETON, AND LIMBS.

THE first trace of the cerebro-spinal axis in the embryo consists of the two longitudinal folds of the external blastodermic layer, including between them the median furrow, known as the "medullary groove" (page 630). When these folds have united on the median line, converting the groove into a canal, the cavity thus produced assumes the name of the "medullary canal," within and around which the central nervous system is formed.

Fig. 217.

Formation of the Cerebro - Spinal Axis. — *a*, *b*. Spinal cord. *c*. Cephalic extremity. *d*. Caudal extremity.

Fig. 219.

Fœtal Pig, 1½ centimetre long, showing the condition of the brain and spinal cord.—1. Hemispheres. 2. Tubercula quadrigemina. 3. Cerebellum. 4. Medulla oblongata.

Fig. 218.

Formation of the Cerebro-Spinal Axis.—1. Vesicle of the hemispheres. 2. Vesicle of the tubercula quadrigemina. 3. Vesicle of the medulla oblongata.

Its mode of formation is by the growth of nervous matter from the inner surface of the medullary canal. The cerebro-spinal axis, accordingly, is at first a hollow longitudinal cord, varying in size in different regions (Fig. 217). Its anterior part expands into a bulbous enlargement corresponding to the brain. Its posterior part, which represents the spinal cord, is nearly cylindrical, terminating at its caudal extremity by a pointed enlargement.

The next change is a division of the anterior bulbous enlargement into three secondary compartments, partially separated from each other by transverse constrictions. They are known as the *cerebral vesicles*, from which the different parts of the encephalon are afterward developed (Fig. 218). The first or most anterior vesicle is destined to form the hemispheres; the second or middle, the tubercula quadrigemina; the third, or posterior, the medulla oblongata. All three vesicles are hollow, and their cavities communicate with each other through the intervening orifices.

Very soon the anterior and posterior cerebral vesicles undergo a further separation. The anterior vesicle is divided into two portions, of which the first, or larger, constitutes the hemispheres, while the second, or smaller, becomes the optic thalami. The third vesicle also separates into two portions, of which the anterior becomes the cerebellum, the posterior the medulla oblongata.

Fig. 220.

Fœtal Pig, three centimetres long.—1. Hemispheres. 2. Tubercula quadrigemina. 3. Cerebellum. 4. Medulla oblongata.

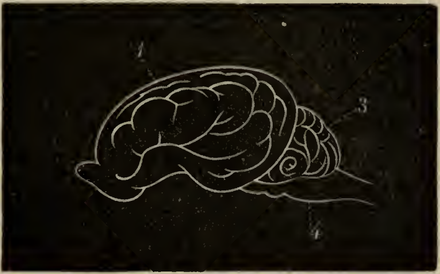
Fig. 221.

Head of Fœtal Pig, nine centimetres long.—1. Hemispheres. 3. Cerebellum. 4. Medulla oblongata.

There are, therefore, at this time five cerebral vesicles, all of which communicate with each other and with the central cavity of the spinal cord. The entire cerebro-spinal axis also becomes strongly curved in an anterior direction, corresponding with the curvature of the body of the embryo (Fig. 219); so that the middle vesicle, or that of the tubercula quadrigemina, occupies a prominent angle at the upper part of the encephalon, while the hemispheres and the medulla oblongata are situated below it, anteriorly and posteriorly. The relative size of the various parts of the encephalon is very different from that in the adult condition. The hemispheres are hardly larger than the tubercula quadrigemina; and the cerebellum is inferior in size to the medulla oblongata. Soon afterward, the relative position and volume of the parts begin to alter. The hemispheres and tubercula quadrigemina grow faster than the posterior portions of the encephalon; and the cerebellum is doubled backward over the medulla oblongata. (Fig. 220.) Subsequently, the hemispheres enlarge more rapidly, growing upward and backward, so as to cover both the optic thalami and the tubercula quadrigemina (Fig. 221); the cerebellum projecting in the same way over the medulla oblongata. The subsequent development of the encephalon is mainly a continuation of the same process; the relative dimensions of the parts constantly changing, so that the hemispheres become, in the adult condition (Fig. 222), the largest division of the encephalon, while the cerebellum is next in size, and covers the upper portion of the medulla oblongata. The hemispheres and cerebellum, which are at first smooth, become afterward convoluted; thus increasing still farther the extent of their nervous matter. In the human fœtus the cerebral convolutions begin to appear about the fifth month (Longet); growing deeper and more abundant during the remainder of fœtal life.

The lateral portions of the brain, enlarging at the same time more rapidly, project on each side outward and upward; and coming in contact with each other along the median line, form the right and left hemispheres, separated by the *longitudinal fissure.* A similar growth in the spinal cord results in the formation of its two lateral halves, separated by the anterior and posterior median fissures. Elsewhere the median fissure is less complete, as, for example, between the two lateral halves of the cerebellum and medulla oblongata; but it exists everywhere, and marks more or less distinctly the division of the nervous centres, produced by the growth of their lateral parts. In this way the whole cerebro-spinal axis is converted into a double organ, equally developed on the right and left sides, and partially divided by longitudinal median fissures.

Fig. 222.



Brain of Adult Pig.—1. Hemispheres. 3. Cerebellum. 4. Medulla oblongata.

Organs of Special Sense.—The eye is formed on each side by a lateral offshoot from the first cerebral vesicle. It is at first a hollow diverticulum, the cavity of which communicates with that of the hemisphere from which it was produced. Afterward, the passage of communication is filled with a deposit of nervous matter, which becomes the *optic nerve.* The globular portion of the diverticulum, which is converted into the eyeball, is lined posteriorly by a thin layer of nervous matter, which becomes the *retina;* its cavity being occupied by a gelatinous substance, the *vitreous body.* The crystalline lens is formed in a distinct follicle, an offshoot of the integument, which becomes partially imbedded in the anterior portion of the eyeball. The cornea is also originally a part of the integument, and remains somewhat opaque until a late period of development. It becomes nearly transparent a short time before birth.

The iris is a muscular septum, formed in front of the crystalline lens. Its central opening, which afterward becomes the pupil, is at first closed by a vascular membrane—the *pupillary membrane,* passing across the longitudinal axis of the eye. The blood-vessels of this membrane, which are derived from those of the iris, subsequently become atrophied. They first disappear from its centre, and recede gradually toward its circumference, returning upon themselves in loops, the convexities of which are directed inward. The pupillary membrane finally becomes atrophied, following in this process its receding blood-vessels from the centre outward. It has completely disappeared by the end of the seventh month. (Cruveilhier.)

The eyelids are formed by folds of the integument, projecting from above and below at the situation of the eyeball. They grow so rapidly during the second and third months that their margins come in contact and adhere together, so that at that time they cannot be separated without violence. They remain adherent until the seventh month (Guy), when they again separate and become movable. In carnivorous animals (dogs and cats), they remain adherent until eight or ten days after birth.

The internal ear is formed by an offshoot from the third cerebral vesicle; the passage of communication afterward filling up by a deposit of white substance, which becomes the auditory nerve. The tympanum and auditory meatus are derived from the external integument.

Skeleton and Limbs.—The spinal column makes its first appearance as a series of cartilaginous rings deposited round the "chorda dorsalis" (page 633). These rings, increasing in thickness by subsequent growth, become the bodies of the vertebræ; from which outgrowths afterward take place in various directions, forming the transverse, oblique, and spinous processes of the vertebræ, and enclosing the spinal canal.

When the union of the dorsal plates on the median line fails to take place, the spinal canal remains open at that situation, and presents the malformation known as *spina bifida.* This may consist simply in a fissure of the spinal canal, more or less extensive, which may sometimes be cured, or even close spontaneously; or it may be complicated with imperfect development or absence of the spinal cord at the same spot, producing permanent paralysis of the lower limbs.

The entire skeleton is at first cartilaginous. The earliest points of ossification show themselves, about the beginning of the second month, almost simultaneously in the clavicle and the lower jaw. Then come, in the following order, the femur, humerus and tibia, the superior maxilla, the bodies of the vertebræ, the ribs, the vault of the cranium, the scapula and pelvis, the metacarpus and metatarsus, and the phalanges of the fingers and toes. The bones of the carpus are all cartilaginous at birth, and begin to ossify only at the end of the first year. According to Cruveilhier, the calcaneum, the cuboid, and sometimes the astragalus, begin their ossification during the latter periods of fœtal life, but the remainder of the tarsus is cartilaginous at birth. The lower extremity of the femur, according to the same authority, shows a point of ossification at birth; all the other extremities of the long bones being still in a cartilaginous condition. The scaphoid bone of the tarsus and the pisiform bone of the carpus are the last to commence their ossification, several years after birth. Nearly all the bones ossify from several distinct points; the ossification spreading as the cartilage increases in size, and the bony pieces, thus produced, uniting with each other at a later period, usually some time after birth.

The limbs appear by a budding process from corresponding parts of the body. They are at first mere rounded elevations, without any separation between the fingers and toes, or distinction between the articulations. Subsequently the free extremity of each limb becomes divided into the phalanges of the fingers or toes; and afterward the articulations of the wrist and ankle, knee and elbow, shoulder and hip, appear successively from below upward.

The lower limbs in man are less rapid in development than the upper. Both the legs and the pelvis are very slightly developed in the early periods of growth, as compared with the spinal column to which they are attached. The inferior extremity of the spinal column, formed by the sacrum and coccyx, projects at first beyond the pelvis, forming a tail, which is curled forward toward the abdomen, and terminates in a pointed extremity. The entire lower half of the body, with the spinal column and appendages, is also twisted, from left to right; so that the pelvis is not only curled forward, but also faces at right angles to the direction of the head and upper part of the body. Subsequently the spinal column becomes straighter and loses its twisted form. At the same time the pelvis and its muscular coverings grow so much faster than the sacrum and coccyx, that the latter become concealed under the adjoining soft parts, and the rudimentary tail disappears.

Fig. 223.

Human Embryo, about one month old.—Showing the large size of the head and upper parts of the body; the twisted form of the spinal column; the rudimentary upper and lower limbs; and the rudimentary tail at the end of the spinal column.

The *integument* of the embryo is at first thin, vascular, and transparent. It afterward becomes thicker, whitish, and more opaque. Even at birth it is considerably more vascular than in the adult condition, and has a strongly marked ruddy color, due to its transparency and the abundance of its capillary blood-vessels. The hairs begin to appear about the middle of intra-uterine life; showing themselves first on the eyebrows, afterward on the scalp, trunk, and limbs. The nails are in process of formation from the third to the fifth month; and, according to Kölliker, are covered with a layer of epidermis until after the latter period. The sebaceous matter of the cutaneous glandules accumulates upon the skin after the sixth month, and forms a whitish, semi-solid, oleaginous layer—the *vernix caseosa*, which is most abundant in the flexures of the joints, between the folds of the integument, behind the ears, and on the scalp.

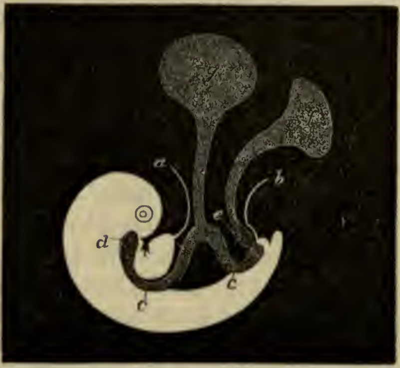
CHAPTER XIV.

DEVELOPMENT OF THE ALIMENTARY CANAL AND APPENDAGES.

THE alimentary canal is formed, as already described (page 621), from the internal blastodermic layer, surrounded by a lamina derived from the mesoderm, which curves downward and inward, and is thus converted into a cylindrical tube, closed at both extremities, and embraced on each side by the abdominal walls. As the abdominal walls do not unite with each other on the median line until after the formation of the intestine, the abdomen of the embryo is at first widely open in front, presenting a long oval excavation, within which the intestinal tube is situated.

Stomach and Intestine.—The formation of the stomach takes place in the following manner: The alimentary canal, originally straight, soon presents two lateral curvatures at the upper part of the abdomen; the first to the left, the second to the right. The first of these curvatures becomes expanded into a wide sac, projecting laterally into the left hypochondrium, and forming the great pouch of the stomach. The second curvature, directed to the right, marks the boundary between the stomach and the duodenum; and the tube at that point, becoming constricted and furnished with an unusually thick layer of muscular fibres, is converted into the pylorus. Immediately below the pylorus, the duodenum again turns to the left; and similar curvatures, increasing in number and complexity, form the convolutions of the small intestine. The large intestine assumes a spiral direction; ascending on the right side, then crossing to the left as the transverse colon, and again descending on the left side, to terminate, through the sigmoid flexure, in the rectum.

FIG. 224.



FORMATION OF THE ALIMENTARY CANAL.—*a*, *b*. Commencement of amnion. *c*, *c*. Intestine. *d*. Pharynx. *e*. Urinary bladder. *f*. Allantois or chorion. *g*. Umbilical vesicle.

The curvatures of the intestinal canal take place in an antero-posterior, as well as in a lateral direction (Fig. 224). The abdominal walls are here imperfectly closed, leaving a wide opening at *a*, *b*, where the integument of the fœtus is continuous with the amnion. The intestine makes at first a single angular turn forward, and at its most prominent portion gives off the stem of the umbilical vesicle (*g*). A short distance below this point it subsequently enlarges in calibre, and the situation of this enlargement marks the commencement of the colon. The two portions of the intestine, after this period, become widely different from each other. The upper portion, which is the small intestine, grows most rapidly in the direction of its length, becoming a long, narrow, convoluted tube; while the lower portion, which is the large intestine, increases mainly in diameter. The lowermost part of the large intestine, which alters least in form and position, becomes the rectum. It elongates comparatively little, retains its position for the most part on the median line, and, as its name indicates, continues nearly straight; presenting only a moderate antero-posterior curvature corresponding with the hollow of the sacrum, and a slight lateral obliquity. It at first forms the blind extremity of the large intestine, but subsequently communicates with the exterior by the perforation of the anus. In the embryo chick, according to Burdach,* the perforation of the anus takes place on the fifth day of incubation; in the human embryo it appears during the seventh week. In certain instances, the opening fails to take place, and the rectum is still closed at birth; presenting the malformation known as *imperforate anus.* If the rectum be otherwise fully developed, it may sometimes be felt, distended with meconium, immediately under the integument; and an artificial opening may be successfully made by incision at the anal region. In other cases the rectum is also more or less deficient, the large intestine terminating in the upper part of the pelvic cavity.

Just beyond the point of junction between the small and the large intestine, the colon presents a rounded diverticulum, which increases in length until the ileum, instead of forming a continuous tube with the colon, seems to join it by an oblique lateral insertion. The diverticulum of the colon is at this time conical in shape; but afterward that portion which forms its free extremity becomes elongated into the appendix vermiformis; while the remaining portion is enlarged into the caput coli.

The caput coli and appendix vermiformis are at first situated near the umbilicus; but between the fourth and fifth months (Cruveilhier) their position is altered, and they become fixed in the right iliac region. During the first six months the internal surface of the small intestine is smooth. At the seventh month the valvulæ conniventes begin to appear, after which they increase in size, though still comparatively undeveloped at birth. The colon is at first smooth and cylindrical in form, like the small intestine; its division into sacculi by longitudinal and transverse bands takes place during the latter half of fœtal life.

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* Traité de Physiologie. Paris, 1838, tome iii., pp. 274, 468.

After the small intestine is formed, it increases rapidly in length. It grows, for a time, faster than the walls of the abdomen; and as it can no longer be contained in the abdominal cavity, it protrudes, under the form of a hernia, from the umbilical opening. (Fig. 225.) In the human embryo, this protrusion continues during the latter part of the second month. Subsequently, the walls of the abdomen grow more rapidly than the intestine; and, gradually enveloping the hernial protrusion, at last reinclose it in the cavity of the abdomen.

Fig. 225.

Fœtal Pig, showing the protruding loop of intestine, forming umbilical hernia. From the convexity of the loop a thin filament is seen passing to the umbilical vesicle, which, in the pig, has a flattened, leaf-like form.

Owing to imperfect development of the abdominal walls, and incomplete closure of the umbilicus, the intestinal protrusion, which is normal during the early stages of fœtal life, sometimes remains at birth, producing *congenital umbilical hernia.* As the parts at this time have a natural tendency to unite with each other, if the hernial protrusion be replaced within the abdomen, and retained there by simple pressure for a sufficient period, the defect is usually remedied, and a cure effected. The conditions are different in the adult, where hernia is usually due to gradual yielding of the fibrous tissues under pressure from within. As the natural period for the closure of the orifices has passed, though the intestine may be retained within the abdomen, in such cases, by mechanical appliances, it again protrudes when they are taken off.

The *contents of the intestine*, which accumulate during fœtal life, vary in different parts of the alimentary canal. In the small intestine they are semifluid in consistency, yellowish or grayish-white in its upper part, yellow, reddish-brown, or greenish-brown below. In the large intestine, where they are of a dark greenish color and pasty in consistency, they have received the name of *meconium*, from their resemblance to inspissated poppy-juice. The meconium contains a large quantity of fat, as well as various insoluble substances, the residue of epithelial and mucous accumulations. It exhibits no trace of the biliary salts (taurocholates and glycocholates) when examined by Pettenkofer's test; and cannot therefore be regarded as an accumulation of bile. In the small intestine, on the contrary, according to Lehmann, slight traces of bile may be detected as early as the fifth or sixth month. We have found distinct indications of bile in the small intestine at birth, but it is always in extremely small quantity, and sometimes altogether absent.

The contents of the fœtal intestine are therefore mainly derived from its mucous membrane. Even their yellowish and greenish hue does not depend on the secretions of the liver, since the yellow color first appears about the middle of the small intestine, and not at its upper extremity. The material which afterward accumulates seems to extend from this point upward and downward, gradually filling the intestine, and becoming, in the ileum and colon, darker colored and more pasty as gestation advances.

The amniotic fluid, during the latter half of fœtal life, finds its way, in greater or less abundance, into the stomach, and thence into the intestine. Small cheesy-looking masses, sometimes found at birth in the fluid contents of the stomach, are seen on microscopic examination to be portions of the vernix caseosa exfoliated from the skin into the amniotic cavity, and afterward introduced through the œsophagus into the stomach. According to Kölliker, the downy hairs of the fœtus, exfoliated from the skin, are often swallowed in the same way, and may be found in the meconium.

The *gastric juice* is not secreted before birth; the fluids of the stomach being generally scanty in amount, clear, nearly colorless, and neutral or alkaline.

Liver.—The liver is developed at a very early period. Its size in proportion to that of the entire body is much greater in the early months than at birth or in the adult condition. In the fœtal pig the relative size of the liver is greatest within the first month, when it amounts to nearly 12 per cent. of the entire bodily weight. Afterward it grows less rapidly than other parts, and its relative weight diminishes successively to 10 per cent. and 6 per cent.; being reduced before birth to 3 or 4 per cent. In man the weight of the liver at birth is also between 3 and 4 per cent. of the entire body.

The *glycogenic function* of the liver commences during fœtal life, and at birth its tissue is abundantly saccharine. In the early periods of fœtal life, however, sugar is produced from other sources than the liver. In very young fœtuses of the pig, both the allantoic and amniotic fluids are saccharine a considerable time before glucose makes its appearance in the hepatic tissue. Even the urine, in half-grown fœtal pigs, contains an appreciable quantity of sugar, and the young animal is normally, at this period, in a diabetic condition. The glucose disappears before birth, as shown by Bernard,* from both the urine and the amniotic fluid; while the liver begins to produce the saccharine substance which it contains after birth.

Lungs, Thorax, and Diaphragm.—The anterior portion of the alimentary canal, which occupies the region of the neck, is the œsophagus. It is straight, and, at first, very short; but it subsequently increases in length, simultaneously with the growth of the neighboring parts. As the œsophagus lengthens, the lungs begin to be developed by a protrusion from its anterior portion, representing the commencement of the trachea. This protrusion soon divides into two symmetrical branches, which, by subsequent elongation and subdivi-

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* Leçons de Physiologie Expérimentale. Paris, 1855, p. 398.

sion, form the bronchial tubes and their ramifications. At first there is no distinction between the chest and abdomen, and the lungs consequently project into the upper part of the abdominal cavity. Afterward, an outgrowth takes place on each side, in the form of a transverse partition, which gradually closes together and becomes the diaphragm, thus shutting off the cavity of the chest from that of the abdomen. Before the closure of the diaphragm, an opening exists by which the peritoneal and pleural cavities communicate with each other. In some instances the development of the diaphragm is arrested at this point, and the opening remains permanent. The abdominal organs then partially protrude into the chest, forming *congenital diaphragmatic hernia.* The lung on the affected side usually remains in a state of imperfect development. Diaphragmatic hernia of this character is more frequently found on the left side than on the right, and may sometimes continue in adult life without causing serious inconvenience.

Urinary Bladder and Urethra.—The urinary bladder originates from an outgrowth of the primitive intestine which at first appears as the allantois (page 641). In the lower animals this outgrowth retains everywhere the character of a hollow sac. In man, that portion which is situated in the body of the embryo and its immediate vicinity is also hollow; while beyond this point it spreads out in the form of a single continuous investing membrane—the "chorion." Its elongated portion, between the chorion and the abdomen of the fœtus, is the "umbilical cord," which at first contains a central tubular canal throughout most of its length. This canal becomes subsequently obliterated; the obliteration commencing at its outer extremity and thence extending inward to the umbilicus. Inside the umbilicus it still proceeds for a certain distance and then ceases. Thus the original protrusion of the intestinal canal within the abdomen, which gave rise to the allantois and chorion, is divided into two portions. The first portion, immediately connected with the intestine, remains hollow, and afterward forms the *urinary bladder.* The second portion, between the urinary bladder and the umbilicus, is consolidated into a rounded cord, termed the *urachus.*

The urinary bladder is at first a pyriform sac (Fig. 224, *e*), communicating at its base with the lower portion of the intestine, and continuous by its pointed extremity with the urachus, by which it is attached to the abdominal walls at the umbilicus. Afterward, the bladder loses this conical figure, and its superior fundus assumes in the adult a rounded form.

Development of the Mouth and Face.—The alimentary canal is at first a cylindrical tube, closed at both extremities. In the region of the abdomen, which in the earlier periods of development occupies nearly the whole of the body, the mesoderm separates, as previously described (page 635), into two laminæ, an outer and an inner. The outer lamina, consisting of the external integument and the subjacent voluntary muscles, forms the parietes of the abdomen. The inner lamina forms the mucous membrane of the alimentary canal, with its covering of involuntary muscular fibres. The separation of these two laminæ leaves between them the peritoneal cavity.

But in the anterior part of the body of the embryo, this separation does not take place. Consequently, that portion of the alimentary canal, namely, the œsophagus, remains in contact with the surrounding parts; and its anterior rounded extremity, the pharynx (Fig. 224, *d*), lies within the head, covered by the united tissues of the middle and external blastodermic layers.

At this time there are formed, on the sides and front of the neck, four nearly transverse fissures, the *cervical fissures*, leading from the exterior into the cavity of the pharynx. These fissures are analogous to the permanent openings at the sides of the neck in fishes, where the gills are located. But in the mammalian embryo they have only a temporary existence. The three lower fissures disappear entirely by the subsequent adhesion of their edges; and in the chick, according to Foster and Balfour, are completely closed by the seventh day of incubation. The upper fissure is converted into a narrow canal, leading into the pharynx, but closed about its middle by a transverse partition. The outer portion of this canal becomes the external auditory meatus; the inner portion, the Eustachian tube. The transverse partition is the membrana tympani.

In the mammalian and human embryo, the bands of solid tissue between the cervical fissures are connected with the formation of the mouth and face. By their increase in growth they become more or less prominent folds, known by the name of the "visceral folds." The first visceral fold grows rapidly forward, and divides into two somewhat diverging processes, which approach each other from the right and left sides toward the median line. The lower pair unite, and form the *inferior maxilla.* The upper pair, which form the *superior maxilla*, unite, not with each other, but with an intervening process which grows from above downward, in the median line, between them.

By the continued growth of these processes, above and below, about the median line, there is included between them a depressed space, lined with a continuation of the integument, and situated immediately in front of the extremity of the pharynx. This excavation is the cavity of the *mouth*, enclosed on each side by the superior and inferior maxillæ; widely open in front, but terminating within by a blind pit, having as yet no communication with the alimentary canal.

Subsequently, an opening is formed between the back part of the mouth and the cavity of the pharynx, by a perforation through the blastodermic tissues at that point. This perforation takes place in the human embryo, according to Burdach,* during the sixth week. The opening thus formed marks the situation of the *fauces;* and the alimentary canal then communicates with the exterior. The epithelium

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* Traité de Physiologie. Paris, 1838, tome iii., p. 468.

of the mouth is consequently derived from the external blastodermic layer, and is originally continuous with the epidermis; while that of the pharynx and œsophagus, like the rest of the intestinal epithelium, is derived from the internal blastodermic layer.

Fig. 226.

Human Embryo, about one month old; showing the growth of the frontal process downward, and that of the superior and inferior maxillary processes from the side. From a specimen in the author's possession.

The completion of the parts about the mouth is accomplished by the continuous development of the processes above described, which grow together in such a way as to diminish the size of the original orifice, and to modify its form in various directions. (Fig. 226.) The process which grows downward in the median line from the frontal region, is called the intermaxillary process, because it intervenes between those forming the superior maxilla, and contains, at a later period, the intermaxillary bones. In quadrupeds the intermaxillary bones, containing the upper incisor teeth, remain distinct from those of the superior maxilla, the line of demarcation between them being indicated by a suture. In man, as a rule, the maxillary and intermaxillary bones are consolidated with each other, the only permanent suture being that on the median line, between the right and left halves of the upper jaw. According to Geoffroy Saint-Hilaire,* a line of suture sometimes remains between the intermaxillary and the superior maxillary bones.

The two inferior maxillary processes unite with each other, making the lower border of the cavity of the mouth, and form, by their union upon the median line, the inferior maxilla. In quadrupeds the inferior maxillary bones present a permanent median suture; but in man they are consolidated into a single piece during the first year after birth.

As the intermaxillary process grows from above downward, it becomes double at its lower extremity, and gives origin to lateral offshoots, which curl round and enclose two circular orifices, the anterior nares (Fig. 227); the offshoots themselves becoming the alæ nasi. Their external border subsequently adheres to the superior maxillary process, leaving only a curvilinear furrow at the side of the nose, to mark the place of consolidation. In many quadrupeds, this furrow remains an open fissure, extending outward and upward from the orifice of the nostril.

The mouth at this time is wide and gaping, owing to the incomplete development of the upper and lower jaw and the comparative insufficiency of the lips and cheeks. The soft parts afterward increase in growth, and thus gradually diminish the size of the orifice (Fig. 228).

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* Histoire des Anomalies de l'Organization. Paris, 1832, tome i., p. 581.

The lips and cheeks arise by folds of the integument and subjacent muscular layers, which, projecting downward, upward, and forward, form the permanent borders of the mouth. The upper lip in man presents a median furrow, bordered by two slightly elevated ridges, corresponding with the union of the maxillary and intermaxillary processes. The lower lip, like the inferior maxilla, is consolidated on the median line, and shows no trace of its double origin.

In some instances, the superior maxillary and intermaxillary processes fail to unite with each other, giving rise to the malformation known as *hare-lip*. The fissure, in cases of hare-lip, is consequently situated, as a rule, not in the median line, but a little on one side, corresponding with the outer edge of the intermaxillary process. Sometimes the deficiency exists on both sides at once, forming "double hare-lip;" in which case, if the fissure extend through the bony structures, the central piece of the superior maxilla, detached from the remainder, contains the upper incisor teeth, and corresponds with the intermaxillary bone of the lower animals. In one instance, observed by Wyman,* the fissure of hare-lip was situated in the median line, the two intermaxillary bones not having united with each other.

Fig. 227.

Head of Human Embryo at about the sixth week. From a specimen in the author's possession.

Fig. 228.

Head of Human Embryo, about the end of the second month. From a specimen in the author's possession.

The eyes at an early period are upon the sides of the head (Fig. 226). As development proceeds, they come to be situated farther forward (Fig. 227), looking obliquely outward. At a still later period they are placed on the anterior plane of the face (Fig. 228), with their axes nearly parallel and looking forward. This change is effected by the more rapid growth of the posterior and lateral portions of the head, which enlarge in such a manner as to alter the relative position of the parts in front.

The palate is formed by the growth of a horizontal partition between the mouth and nares, which arises on each side as an offshoot from the superior maxilla. The two plates afterward unite on the median line,

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* Transactions of the Boston Society for Medical Improvement, March 9th, 1863.

forming a complete separation between the oral and nasal cavities. The right and left nasal passages are separated from each other by a vertical plate (vomer), which grows from above and fuses with the palatal plates below. *Fissure of the palate* is caused by a deficiency of one of the horizontal plates. It is accordingly situated a little on one side of the median line, and is frequently associated with hare-lip and fissure of the upper jaw.

The anterior and posterior arches of the palate are incomplete transverse partitions which grow from the sides of the fauces, subsequently to the perforation of the pharynx and its communication with the oral cavity. Owing to the muscular tissue which they contain, the orifice of the alimentary canal thus becomes capable of constriction or enlargement, according to its condition of functional activity.

CHAPTER XV.

DEVELOPMENT OF THE WOLFFIAN BODIES, KIDNEYS, AND INTERNAL ORGANS OF GENERATION.

THE first trace of a urinary apparatus consists of two elongated, fusiform organs, which make their appearance in the abdomen at a very early period, one on each side the spinal column, known as the *Wolffian bodies.* They are fully formed, in the human embryo, toward the end of the first month (Coste), at which time they are the largest organs in the abdomen, extending from just below the heart nearly to the posterior extremity of the body. In the fœtal pig, when thirteen or fourteen millimetres in length, they are rounded and kidney-shaped, and occupy a large part of the abdominal cavity. Their combined weight is a little over three per cent. of the entire body; a proportion seven or eight times as large as that of the kidneys in the adult condition. There are at this period only three organs of noticeable size in the abdomen, namely, the liver, at the upper part of the abdominal cavity; the intestine, which is already somewhat convoluted, and occupies a central position; and the Wolffian bodies on each side the spinal column.

FIG. 229.

FŒTAL PIG, 13 millimetres long; the abdominal walls cut away, to show the position of the Wolffian bodies.—1. Heart. 2. Anterior limb. 3. Posterior limb. 4. Wolffian body.

The Wolffian bodies, in their intimate structure, closely resemble the adult kidney. They consist of secreting tubules, lined with epithelium, running transversely to the outer edges of the organs, where they terminate by rounded dilatations. In each of these dilated extremities is a globular coil of capillary blood-vessels, similar to the *glomerulus* of the kidney. At the inner edge of the Wolffian body the tubules empty into a common excretory duct, which leaves the organ at its lower extremity, and communicates with the intestinal canal, at a point where the urinary bladder is afterward situated. The principal distinction in structure, between the Wolffian bodies and the kidneys, consists in the size of their tubules and glomeruli. In the fœtal pig, when three or four centimetres in length, the tubules of the Wolffian body are 0.125 millimetre in diameter; while those of the kidney in the same fœtus are only 0.034 millimetre. The glomeruli of the Wolffian bodies are 0.55 millimetre in diameter, while those of the kidney measure only 0.14 millimetre. The Wolffian bodies are therefore urinary organs, so far as regards their minute structure, and are sometimes known by the name of the "false kidneys." There is little doubt that they perform, at this period, a function analogous to that of the kidneys, and separate from the blood of the embryo an excrementitious fluid which is discharged into the cavity of the allantois.

Subsequently, the Wolffian bodies increase in size; but as they grow less rapidly than the other organs, their relative magnitude diminishes. Still later, they suffer an absolute atrophy, and become less perceptible. In the human embryo, they are hardly visible after the second month (Longet), and in the quadrupeds they disappear long before birth.

The *kidneys* are formed just behind the Wolffian bodies, by which they are at first concealed in a front view, the kidneys being at this time not more than one-fourth or one-fifth part the size of the Wolffian bodies. (Fig. 230.) The kidneys subsequently enlarging, while the Wolffian bodies diminish, the proportion between the two organs is reversed; and the Wolffian bodies appear as small ovoid or fusiform masses, on the anterior surface of the kidneys (Figs. 231 and 232). As the kidneys grow more rapidly in an upward than a downward direction, the Wolffian bodies come to be situated near their inferior extremity.

FIG. 230.

FŒTAL PIG, 3½ centimetres long.—1. Wolffian body. 2. Kidney.

The kidneys, during the succeeding periods of fœtal life, become very largely developed in proportion to the rest of the internal organs; attaining a size, in the fœtal pig, equal to more than two per cent. of the entire body. This proportion again diminishes before birth, owing to the increased development of other parts. In the human fœtus at birth, the weight of the two kidneys together is six parts per thousand of the entire body.

Internal Organs of Generation.—About the same time with the formation of the kidneys, two oval-shaped organs make their appearance in front, on the inner side of the Wolffian bodies. These are the internal organs of generation; namely, the testicles in the male, and the ovaries in the female. At first they occupy the same situation and present the same appearance, whether the fœtus be male or female (Fig. 231).

A short distance above the internal organs of generation there commences, on each side, a narrow tube which runs downward, parallel with the excretory duct of the Wolffian body. The two tubes approach each other below; and, joining upon the median line, empty into the base of the allantois, or what will afterward be the urinary bladder. These tubes serve as the excretory ducts of the internal organs of generation; afterward becoming the *vasa deferentia* in the male, and the *Fallopian tubes* in the female. According to Coste, the vasa deferentia at an early period are disconnected from the testicles; originating, like the Fallopian tubes, by free extremities, with an open orifice. Afterward they become adherent to the testicles, and establish a communication with the tubuli seminiferi. In the human female, the Fallopian tube remains disconnected from the ovary, except at one point of its fimbriated extremity; but in many animals the greater part of this extremity becomes adherent to the ovary, which it envelops more or less completely in a distinct sac.

Fig. 231.

Internal Organs of Generation, in a fœtal pig 7½ centimetres long.—1, 1. Kidneys. 2, 2. Wolffian bodies. 3, 3. Internal organs of generation; testicles or ovaries. 4. Urinary bladder, turned over in front. 5. Intestine.

Male Organs of Generation; Descent of the Testicles.—In the male fœtus there now commences a change in position of the internal organs of generation, known as the "descent of the testicles." In consequence of this change, the testicles, which are at first in front of the kidneys, near the middle of the abdomen, come to be situated in the scrotum, outside the abdominal cavity, and enclosed in a distinct sac, the tunica vaginalis testis. This apparent movement results from a disproportionate growth of the abdominal organs above the testicles, by which their relative position becomes altered.

By the upward enlargement of the kidneys, both the Wolffian bodies and the testicles are made to occupy an inferior position (Fig. 232). At the same time, a slender rounded cord (not represented in the figure) passes from the lower extremity of each testicle outward and downward, crossing the vas deferens a short distance above its union with that of the opposite side. Below this point, the cord spoken of continues to run obliquely outward and downward; and, passing through the inguinal canal, is inserted into the subcutaneous tissue near the symphysis pubis. The lower part of this cord becomes the *gubernaculum testis.* It contains muscular fibres, which are easily detected, in the human fœtus, during the latter half of intra-uterine life. At the period of birth, or soon after, they have usually disappeared.

Fig. 232.

Internal Organs of Generation in a fœtal pig nearly 10 centimetres long.—1, 1. Kidneys. 2, 2. Wolffian bodies. 3, 3. Testicles. 4. Urinary bladder. 5. Intestine.

That portion of the excretory tube of the testicle situated outside the crossing of the gubernaculum, becomes afterward convoluted, and converted into the *epididymis.* Inside this point the tube remains comparatively straight, but increases in length, and is finally known as the *vas deferens.*

As the testicles descend still farther in the abdomen, they continue to grow, while the Wolffian bodies become smaller; and at last, when the testicles have arrived at the internal inguinal ring, the Wolffian bodies are no longer recognizable. In the human fœtus, the testicles reach the internal inguinal ring about the end of the sixth month (Wilson).

During the seventh month a protrusion of the peritoneum takes place through the inguinal canal, in advance of the testicle; and as this organ passes into the scrotum, loops of muscular fibres are given off from the lower border of the internal oblique muscle of the abdomen, extending downward over the testicle and spermatic cord. They form afterward the *cremaster muscle.*

At last, the testicles descend quite to the bottom of the scrotum. The convoluted portion of the efferent duct, namely, the epididymis, remains attached to the testicle; while the vas deferens passes upward, in a reverse direction, enters the abdomen through the inguinal canal, again bends downward, and joins its fellow of the opposite side; after which they both open into the prostatic portion of the urethra by distinct orifices, on either side of the median line. At the same time, two diverticula arise from the median portion of the vasa deferentia, and, elongating in a backward direction, beneath the base of the bladder, become developed into sacculated reservoirs, the *vesiculæ seminales.*

The left testicle is a little later in its descent than the right; but it passes farther into the scrotum, and, in the adult condition, usually hangs lower than that of the opposite side.

Fig. 233.

Formation of the Tunica Vaginalis Testis.—1. Testicle nearly at the bottom of the scrotum. 2. Cavity of tunica vaginalis. 3. Cavity of peritoneum. 4. Obliterated neck of peritoneal sac.

After the testicle has passed into the scrotum, the serous pouch, which preceded its descent, remains for a time in communication with the general cavity of the peritoneum. In many quadrupeds, as, for example, the rabbit, this condition is permanent; and the testicle may be either drawn downward into the scrotum, or retracted into the abdomen, by the alternate action of the gubernaculum and the cremaster muscle. In the human fœtus the opposite surfaces of the peritoneal pouch approach each other at the inguinal canal, forming a constriction, which partly shuts off the testicle from the cavity of the abdomen. By a continuation of this process, the serous surfaces come in contact, and, adhering together at this situation (Fig. 233, $_4$), form a kind of cicatrix, by which the cavity of the tunica vaginalis ($_2$) is shut off from the general cavity of the peritoneum ($_3$). The tunica vaginalis testis is, therefore, originally a part of the peritoneum, from which it is subsequently separated by the constriction and adhesion of its opposite walls.

The separation of the tunica vaginalis testis from the peritoneum is usually complete in the human fœtus before birth. But sometimes it fails to take place at the usual time, and the intestine is then liable to protrude into the scrotum, in front of the spermatic cord, giving rise to *congenital inguinal hernia.* (Fig. 234.) The parts implicated in this malformation have still a tendency to unite; and if the intestine be retained by pressure within the abdomen, cicatrization usually takes place at the inguinal canal, and a cure is effected.

FIG. 234.

CONGENITAL INGUINAL HERNIA. —1. Testicle. 2, 2, 2. Intestine.

Female Organs of Generation.—At an early period of development the ovaries have the same external appearance, and occupy the same position in the abdomen, as the testicles in the opposite sex. The descent of the ovaries also takes place, to a great extent, in the same way with that of the testicles. When, in the early part of this descent, they reach the lower edge of the kidneys, a cord, analogous to the gubernaculum testis, extends from their lower extremity, downward and forward, to the subcutaneous tissues at the inguinal ring. That part of the efferent duct situated outside the crossing of this cord becomes convoluted, and is converted into the *Fallopian tube;* while that inside the same point is developed into the *uterus.* The upper portion of the cord becomes the *ligament of the ovary;* its lower portion, the *round ligament of the uterus.*

As the ovaries continue their descent, they pass below and behind the Fallopian tubes, which perform at the same time a movement of rotation, backward and downward; the whole, together with the ligaments of the ovaries and the round ligaments, being enveloped in folds of peritoneum, which enlarge with the growth of the included parts, and constitute finally the *broad ligaments of the uterus.*

During these changes in the adjacent organs, the two lateral halves of the uterus fuse with each other on the median line, and become covered with muscular fibres. In quadrupeds, the uterus remains divided for the most part into two long conical tubes or cornua (Fig. 164). In the human species, the fusion between the lateral halves of the organ is nearly complete; so that the uterus presents externally a rounded, flattened, and somewhat triangular figure, with the ligaments of the ovary and the round ligaments passing off from its upper corners. Internally, its cavity still presents a strongly marked triangular form, the vestige of its original division.

Occasionally the human uterus remains divided internally by a vertical septum, running from the middle of its fundus toward the os internum. It may even present a partial external division, corresponding with the situation of the septum, and producing the malformation known as *uterus bicornis*, or double uterus.

The os internum and os externum are produced by partial constrictions of the original generative passage; and the distinctions between the body of the uterus, the cervix, and the vagina, arise from the different development of its mucous membrane and muscular tunic in the corresponding parts. During fœtal life the neck of the uterus grows faster than its body; so that at birth the cervix uteri constitutes nearly two-thirds of the entire organ; while the body forms but little over one-third. The cervix, at this time, is also wider than the body; so that the whole organ presents a tapering form from below upward. The arbor vitæ uterina of the cervix is at birth very fully developed, and the mucous membrane of the body is thrown into three or four folds which radiate upward from the os internum. The cavity of the cervix is filled with transparent semi-solid mucus.

The position of the uterus at birth is different from that in adult life; nearly the entire organ being above the symphysis pubis, and its inferior extremity passing below that level only by about six millimetres. It is also slightly anteflexed at the junction of the body and cervix. After birth, the uterus with its appendages continues to descend; and at puberty its fundus is just below the level of the symphysis pubis.

The *ovaries* at birth are narrow and elongated in form. They contain an abundance of eggs; each enclosed in a Graafian follicle, and averaging .04 millimetre in diameter. The vitellus in most is imperfectly formed, and in some is hardly distinguishable. The Graafian follicle at this period contains no fluid, but only the egg and the layer of cells forming the "membrana granulosa." Inside this layer is to be seen the germinative vesicle, with the germinative spot, surrounded by a faintly granular vitellus, more or less abundant in different parts of the ovary. Some of the Graafian follicles containing eggs are as large as .05 millimetre; others as small as .02 millimetre. In the very smallest the cells of the membrana granulosa appear to fill the cavity of the follicle, concealing the rudiments of the primitive egg.

CHAPTER XVI.

DEVELOPMENT OF THE VASCULAR SYSTEM.

THE vascular system presents itself, during different periods of life, under three distinct forms, which follow each other in the progress of development, as different organs are employed in the functions of nutrition. The first form is that of the *vitelline circulation*, which exists at a period when the vitellus is the source of nutrition for the embryo. The second is the *placental circulation*, in which the materials of nourishment are supplied by the placenta, and which lasts through the greater part of fœtal life. The third is the *adult circulation*, in which nutrition and the renovation of the blood are provided for by the lungs and the intestinal canal.

Vitelline Circulation.—When the body of the embryo has begun to be formed in the centre of the blastoderm, a number of blood-vessels shoot out from its sides and ramify over the neighboring parts of the vitelline sac, forming by their inosculation the plexus of the area vasculosa. In the egg of the fish (Fig. 235), the area vasculosa occupies the whole surface of the vitellus, outside the body of the embryo. A number of arteries pass out from each side, supplying the vascular network; and the blood is returned to the embryo by an anterior vitelline vein, passing upward along the front of the egg, and entering the body beneath the head.

FIG. 235.

EGG OF FISH (Jarrabacca), showing the vitelline circulation.

In the egg of the fowl (page 636), the area vasculosa spreads gradually over the vitelline sac from within outward. During this extension some of its vessels change in relative size and importance. The vena terminalis, forming its outer border, becomes less distinct; and, in addition to the anterior and lateral vitelline veins, in front and on the sides, there is also a "posterior vitelline vein," coming from the hinder part of the area vasculosa and reaching the embryo beneath its caudal extremity.

In man and mammalians, the first formation of the area vasculosa is similar to that in fishes and birds. But owing to the small size and rapid exhaustion of the vitellus as a source of nourishment, this form of the circulation never acquires a high degree of development, and soon becomes retrograde. It presents, however, certain modifications, connected with the origin of various parts of the permanent vascular system.

These modifications relate mainly to the vessels distributing the blood to the external vascular plexus, and returning it thence to the embryo. As the embryo and the entire egg increase in size, two arteries and two veins become larger than the rest, and subsequently do the whole work of conveying the blood to and from the area vasculosa. The arteries emerge from the lateral edges of the embryo, on the right and left sides; while the veins re-enter at about the same point and nearly parallel with them. These four vessels are termed the *omphalo-mesenteric arteries and veins.*

The arrangement of the circulatory apparatus in the interior of the body at this time is as follows: The heart is situated at the median line, immediately beneath the head, and in front of the œsophagus. It receives at its lower extremity the united trunks of the two omphalo-mesenteric veins, and at its upper extremity gives off two vessels which almost immediately divide into two sets of lateral arches, bending backward along the sides of the neck, and reuniting into two trunks in front of the vertebral column. These trunks then run from above downward on each side the median line. They are called the *vertebral arteries*, on account of their situation, adjacent to and parallel with the vertebral column. They give off, throughout their course, small lateral branches, which supply the body of the embryo, and also two larger branches—the omphalo-mesenteric arteries—which pass out, as above described, to the area vasculosa. The two vertebral arteries remain separate in the upper part of the body, but fuse with each other a little below the level of the heart; so that, beyond this point, there remains but one large artery—the aorta—running from above downward along the median line, giving off the omphalo-mesenteric arteries to the area vasculosa, and supplying smaller branches to the body, the walls of the intestine, and the other organs of the embryo.

FIG. 236.

Diagram of the EMBRYO AND ITS VESSELS, showing the circulation of the umbilical vesicle; and also that of the allantois, beginning to be formed.

This is the condition which marks the first or vitelline circulation. A change now begins to take place, in which the vitellus is superseded, as an organ of nutrition, by the placenta; giving rise to the second or *placental* circulation.

Placental Circulation.—After the umbilical vesicle has been formed by the process already described (page 639), a part of the vitellus remains included in it, while the rest is retained in the abdomen, enclosed in the intestinal canal. As these two organs (umbilical vesicle and intestine) are originally parts of the same vitelline sac, they remain supplied by the same vascular system, namely, the omphalo-mesenteric vessels. Those within the abdomen supply the mesentery and intestine; while the remainder pass outward and ramify on the walls of the umbilical vesicle (Fig. 236). At first there are, as above mentioned, two omphalo-mesenteric arteries emerging from the body, and two omphalo-mesenteric veins returning to it; but afterward the two arteries are replaced by a common trunk, while a similar change takes place in the veins. Subsequently, therefore, there remain but one artery and one vein, connecting the internal and external portions of the vitelline circulation.

The vessels belonging to this system are called the omphalo-mesenteric vessels, because a part of them (omphalic vessels) pass outward, by the umbilicus, or "omphalos," to the umbilical vesicle, while the remainder (mesenteric vessels) ramify upon the mesentery and the intestine.

FIG. 237.

Diagram of the EMBRYO AND ITS VESSELS, showing the second or placental circulation. The intestine has become further developed, and the mesenteric arteries have enlarged, while the umbilical vesicle and its vascular branches are reduced in size. The large umbilical arteries are seen passing out to the placenta.

At first, the circulation of the umbilical vesicle is more important than that of the intestine; and the omphalic artery and vein appear accordingly as large trunks, of which the mesenteric vessels are small branches (Fig. 236). Afterward the intestine enlarges, while the umbilical vesicle diminishes, and the proportion between the two sets of vessels is reversed. The mesenteric vessels then come to be the principal trunks, while the omphalic vessels are minute branches, running out to the umbilical vesicle, and ramifying in a few scanty twigs upon its surface (Fig. 237).

In the meantime, the allantois is formed by a protrusion from the lower extremity of the intestine, which, carrying with it two arteries and two veins, passes out from the abdomen, and comes in contact with the external membrane of the egg. The arteries of the allantois, termed the *umbilical arteries*, are supplied by branches of the abdominal aorta; while the venous trunks returning from it, or the *umbilical veins*, join the mesenteric veins, and empty with them into the venous extremity of the heart. As the umbilical vesicle diminishes, the allantois enlarges; and the latter is converted, in the human subject, into a vascular chorion, which serves for the formation of the placenta (Fig. 237). As the placenta soon becomes the only source of nutrition for the fœtus, its vessels increase in size, and preponderate over all other parts of the circulatory system. During the early periods of its formation there are, as above mentioned, two umbilical arteries and two umbilical veins. Subsequently one of the veins disappears, while the other becomes enlarged in proportion, and returns the whole of the blood from the placenta to the fœtus. For a long time previous to birth the umbilical cord contains therefore two umbilical arteries, and but one umbilical vein.

Adult Circulation.—The placental circulation is exchanged at birth for the third or adult circulation. This is distinguished by the disappearance of the placenta and the vessels connected with it, and by the entrance into activity of the lungs and the alimentary canal, as the organs of nutrition and aeration. A large proportion of the blood is accordingly turned away from its former channels, and distributed to new organs. This change is comparatively rapid. The previous transition, from the vitelline to the placental circulation, was gradual; the umbilical vesicle diminishing simultaneously with the enlargement of the placenta, and the two organs, with their blood-vessels, coëxisting for a certain period. But at birth the placenta is suddenly withdrawn from the circulatory system and replaced in functional activity by the lungs and the alimentary canal.

This change, however, has been already provided for by the gradual development of the necessary organs, and by corresponding alterations in both the arterial and venous systems.

Development of the Arterial System.—At an early period of development, the arterial trunks, after passing off from the anterior extremity of the heart, curve backward, as already described (page 688), in two sets of lateral branches, toward the vertebral column, after which they reunite, to form the "vertebral arteries." The curved branches, embracing the sides of the neck, are called the *cervical arches.* They pass through the substance of the "visceral folds," already described (page 677), and are separated from each other by the intervening cervical fissures. In the embryo chick, according to Foster and Balfour, three cervical arches, in the three upper visceral folds, have been formed by the end of the second day of incubation. During the third and fourth days, the first and second cervical arches become obliterated, a fourth and a fifth appearing at the same time, in the corresponding visceral folds. Thus there are, in all, five vascular cervical arches; but only three are to be found coëxisting at any one time.

In fishes, the cervical arches remain as permanent blood-vessels supplying the gills, four or five in number on each side. In birds and mammalians, some of the cervical arches disappear, or leave only certain arterial inosculations as vestiges of their embryonic existence. Some, on the other hand, remain as permanent vascular trunks or branches, forming important parts of the adult arterial system.

The details of growth and modification in the cervical arches are not all described in the same manner by different observers; and there seems to be some difference, in this respect, between mammalians and birds. The general features of the process, however, are as follows:

The two ascending trunks, on the anterior part of the neck, from which the cervical arches are given off, become the carotid arteries. The first and second, that is, the two upper cervical arches, on each side, disappear completely, or remain only as small and inconstant arterial inosculations. The third arch becomes the subclavian artery, giving off the permanent vertebral artery, and continuing its course as the axillary artery, to the upper limb. The fourth cervical arch undergoes different changes on the two sides. On the left side it becomes enormously enlarged, giving off, as secondary branches, all the arterial trunks going to the head and upper limbs, and is thus converted into the *arch of the aorta*. On the right side it grows smaller, and ultimately disappears; so that at last there is only a single aortic arch, situated on the left of the median line, and continuous below with the thoracic aorta.

The fifth or last cervical arch becomes on each side the pulmonary artery; its external portion on the right side disappearing at a very early period, but on the left remaining for a certain time, as the ductus arteriosus, between the pulmonary artery and the aorta.

Notwithstanding that all the cervical arches are at first, as their name implies, situated in the region of the neck, their remains or permanent representatives in the complete form of the arterial system, come to be placed farther downward, and even in the cavity of the chest. This is due to the varying rapidity of growth in different parts, at successive periods of development. The thorax at first has no existence as a distinct portion of the trunk; the heart being placed immediately beneath the head, and afterward changing its position with the increasing development of the lungs and chest. The neck, with the œsophagus and trachea, also elongates in an upward direction, so that the vascular organs of this region afterward occupy a situation farther down. In fishes, where there are no lungs and no thoracic cavity, the cervical arches are permanent, and the heart remains in the anterior portion of the trunk, just behind the gills.

Corresponding changes take place, during this time, in the lower part of the body. Here the abdominal aorta runs undivided, on the median line, to the end of the spinal column; giving off lateral branches to the intestine and the abdominal walls. When the allantois is developed, two of these branches accompany it, and become, consequently, the umbilical arteries. These vessels increase so rapidly in size, that they soon appear as main divisions of the aorta; while its original continuation, running to the end of the spinal column, appears as a small branch given off at the point of bifurcation. The lower limbs are supplied by two small branches from the umbilical arteries near their origin.

Up to this time, the pelvis and lower limbs are but slightly developed. Subsequently they grow more rapidly, in proportion to the rest of the body, and their arteries enlarge to a corresponding degree. That portion of the umbilical arteries lying between the bifurcation of the aorta and the branches going to the lower limbs, becomes the common iliac arteries, which afterward divide into the umbilical arteries proper and the femorals. Subsequently, in accordance with the growth of the pelvis and lower limbs, the relative size of their blood-vessels is still further increased; and at last the arterial system in this part of the body assumes the arrangement belonging to the latter periods of gestation. The aorta divides, as before, into the two common iliac arteries. These divide into the external iliacs, supplying the lower limbs, and the internal iliacs, supplying the pelvis; and this division is so placed that the umbilical arteries arise from the internal iliacs, of which they now appear to be secondary branches.

After birth, the umbilical arteries become for the most part atrophied, and are converted, in the adult condition, into solid cords, running upward to the umbilicus. Their lower portions, however, remain pervious, under the name of the "hypogastric arteries," and give off branches supplying the urinary bladder. The terminal continuation of the original abdominal aorta is the arteria sacra media, which, in the adult, runs downward on the anterior surface of the sacrum, supplying the rectum and the anterior sacral nerves.

Development of the Venous System.—According to Coste, the principal veins of the body consist at first of two long venous trunks, the *vertebral veins* (Fig. 238), running along the sides of the vertebral column, parallel with the vertebral arteries. They receive in succession all the intercostal veins, and empty into the heart by two lateral trunks, the *canals of Cuvier*. When the lower limbs become developed, their two veins join the vertebral veins in the posterior portion of the body; and, crossing them, afterward unite with each other, constituting a third vein of new formation (Fig. 239, *a*), which runs upward a little to the right of the median line, and empties by itself into the lower extremity of the heart.

The two branches which thus unite become afterward the common iliac veins; and the trunk resulting from their union is the *vena cava inferior*. Subsequently, the vena cava inferior becomes very much larger than the vertebral veins, and returns to the heart nearly all the blood from the lower half of the body.

Above the level of the heart the vertebral and intercostal veins retain their relative size until the development of the upper limbs has commenced. Then two of the intercostal veins increase in diameter (Fig. 240), and become the right and left subclavians; while the vertebral veins situated above them become the right and left jugular veins. Just below the junction of the jugulars with the subclavians, a small branch of communication now appears between the two vertebrals (Fig. 239, *b*), passing from left to right, and emptying into the right vertebral vein a little above the heart; so that a part of the blood coming from the left side of the head, and the left upper limb, still passes down the left vertebral vein to the heart on its own side, while a part crosses over by the communicating branch (*b*), and reaches the heart through the right vertebral vein. Soon afterward, this branch of communication enlarges so rapidly that it preponderates over the vertebral vein from which it originated (Fig. 240), and becomes the left *vena innominata.*

Fig. 238.

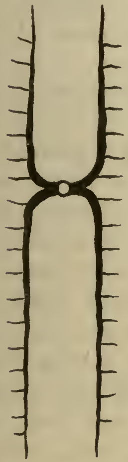
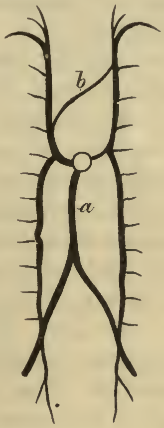


Diagram of the Venous System in its early condition; showing the vertebral veins emptying into the heart by two lateral trunks, the "canals of Cuvier."

Fig. 239.



Venous System farther advanced, showing the iliac and subclavian veins. — *a.* Vein of new formation, which becomes the inferior vena cava. *b.* Transverse branch of new formation, which becomes the left vena innominata.

Fig. 240.

Further development of the Venous System.—The vertebral veins are reduced in size, and the canal of Cuvier, on the left side, is disappearing. *c.* Transverse branch of new formation, which becomes the vena azygos minor.

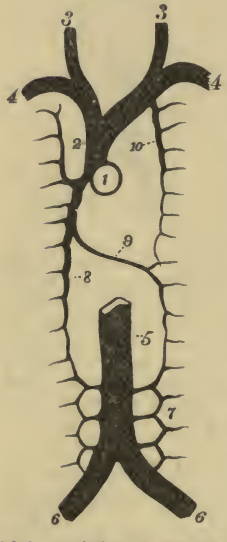
On the left side, that portion of the superior vertebral vein, which is below the subclavian, remains as a branch of the vena innominata, receiving the six or seven upper intercostal veins; while on the right side it becomes excessively enlarged, receiving the blood of both jugular and both subclavian veins, and is converted into the *vena cava superior.*

The left canal of Cuvier, by which the left vertebral vein at first communicates with the heart, is subsequently obliterated, while that on the right side becomes excessively enlarged, forming the lower extremity of the vena cava superior.

The superior and inferior venæ cavæ, accordingly, do not correspond with each other so far as regards their origin. The superior vena cava is one of the original vertebral veins; while the inferior vena cava is a vessel of new formation, resulting from the union of two lateral trunks from the inferior limbs.

The remaining vertebral veins finally assume the condition shown in Fig. 241, which is the adult form of the venous circulation. At the lower part of the abdomen the vertebral veins send inward transverse branches of communication to the vena cava inferior, between the points at which they receive the intercostal veins. These branches of communication become the *lumbar veins* ($_{7}$), which in the adult communicate with each other by arched branches, a short distance to the side of the vena cava. Above the level of the lumbar arches, the vertebral veins retain their original direction. That upon the right side still receives all the right intercostal veins, and becomes the *vena azygos major* ($_{8}$). It also receives from its fellow of the left side a small branch of communication (Fig. 240, *c*), which soon enlarges to such an extent as to bring over to the vena azygos major all the blood of the five or six lower intercostal veins of the left side, becoming, in this way, the *vena azygos minor* (Fig. 241, $_{9}$). The six or seven upper intercostal veins on the left side still empty, as before, into their own vertebral vein ($_{10}$), which, joining the left vena innominata above, is known as the *superior intercostal vein.* The left canal of Cuvier has by this time disappeared; so that all the venous blood now enters the heart by the superior and the inferior vena cava. But the original vertebral veins are still continuous throughout, though much diminished in size at certain points; since both the greater and lesser azygous veins inosculate below with the superior lumbar veins, and the superior intercostal vein inosculates below with the lesser azygous vein, before it crosses to the right side.

FIG. 241.



Adult condition of the VENOUS SYSTEM. — 1. Right auricle of the heart. 2. Vena cava superior. 3, 3. Jugular veins. 4, 4. Subclavian veins. 5. Vena cava inferior. 6, 6. Iliac veins. 7. Lumbar veins. 8. Vena azygos major. 9. Vena azygos minor. 10. Superior intercostal vein.

There are two parts of the circulatory apparatus, the development of which is sufficiently important to be described separately. These are, first, the liver and the ductus venosus, and secondly, the heart and ductus arteriosus.

The Hepatic Circulation and Ductus Venosus.—The liver appears at a very early period, in the upper part of the abdomen, as a mass of glandular and vascular tissue, developed around the upper portion of the omphalo-mesenteric vein, just below its termination in the heart (Fig. 242). As soon as the organ has attained a considerable size, the omphalo-mesenteric vein ($_1$) breaks up in its interior into a capillary plexus, the vessels of which reunite into a venous trunk, conveying the blood toward the heart. The omphalo-mesenteric vein below the liver then becomes the *portal vein;* while above that organ it receives the name of the *hepatic vein* ($_2$). The liver, accordingly, is at this time supplied with blood entirely by the portal vein, coming from the umbilical vesicle and the intestine; and all the blood derived from this source passes through the hepatic circulation before reaching the heart.

FIG. 242.

Early form of the HEPATIC CIRCULATION. — 1. Omphalo-mesenteric vein. 2. Hepatic vein. 3. Heart. The dotted line shows the situation of the future umbilical vein.

But soon afterward the allantois makes its appearance, and becomes developed into the placenta; and the umbilical vein returning from it joins the omphalo-mesenteric vein, and takes part in the formation of the hepatic capillary plexus. Since the umbilical vesicle, however, becomes atrophied and the intestine remains inactive, while the placenta increases in size and importance, a period arrives when the liver receives more blood by the umbilical vein than by the portal vein (Fig. 243). The umbilical vein then passes into the liver at the longitudinal fissure, and ramifies throughout the left lobe of the organ. To the right it sends a large branch of communication, which opens into the portal vein, and partially provides for the circulation in the right lobe. The liver is thus supplied with blood from two sources, the most abundant of which is the umbilical vein; while all the blood which enters it circulates, as before, through its capillary vessels.

FIG. 243.

HEPATIC CIRCULATION farther advanced.—1. Portal vein. 2. Umbilical vein. 3. Hepatic vein.

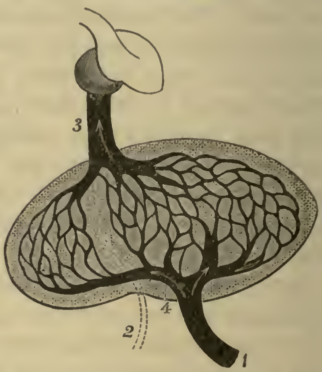
But the liver at this time is much larger, in proportion to the other organs, than at a later period. In the fœtal pig, when very young, it amounts to nearly twelve per cent. of the whole body; while before birth it diminishes to seven, six, and even three or four per cent. In the latter part of fœtal life, therefore, its capillary circulation becomes insufficient to accommodate all the blood returning from the placenta; and a vascular canal is formed in its interior, by which a portion of the placental blood reaches the heart without passing through the hepatic capillaries. This canal is the *Ductus venosus.*

The ductus venosus is formed by a dilatation of one of the hepatic capillaries (Fig. 244), which is thus converted into a wide branch of communication between the umbilical vein below and the hepatic vein above. The circulation in the liver, at this period, is as follows: A certain quantity of venous blood still enters through the portal vein ($_1$), and circulates in a part of the capillary system of the right lobe. The umbilical vein ($_2$) enters the liver a little to the left, bringing a larger quantity of blood, which divides into three principal streams. One of them passes through the left branch of the umbilical vein ($_3$) into the capillaries of the left lobe; another turns off through the right branch ($_4$), and, joining the blood of the portal vein, circulates through the capillaries of the right lobe; while the third passes through the ductus venosus ($_5$) to the hepatic vein without traversing any part of the capillary plexus.

Fig. 244.

Hepatic Circulation during the latter part of fœtal life.—1. Portal vein. 2. Umbilical vein. 3. Left branch of umbilical vein. 4. Right branch of umbilical vein. 5. Ductus venosus. 6. Hepatic vein.

Fig. 245.



Adult Form of Hepatic Circulation.—1. Portal vein. 2. Obliterated umbilical vein, forming the round ligament; the continuation of the dotted lines through the liver shows the situation of the obliterated ductus venosus. 3. Hepatic vein. 4. Left branch of portal vein.

This form of the hepatic circulation continues until birth. At that time, two important changes take place. First, the placental circulation is cut off; and secondly, a much larger quantity of blood than before is supplied to the lungs and the intestine. The superabundant blood, previously circulating in the placenta, is now diverted to the lungs; while the intestinal canal becomes the only source of venous supply for the hepatic blood. The following changes, therefore, take place in the liver (Fig. 245). First, the umbilical vein shrivels and becomes impervious. It remains in this condition, in the adult, as the *round ligament* ($_2$), extending from the inner surface of the abdominal walls, at the umbilicus, to the longitudinal fissure of the liver. Secondly, the ductus venosus is also obliterated. Thirdly, the blood entering the liver by the portal vein ($_1$) passes by its right branch, as before, to the right lobe. But in its left branch ($_4$) the course of the blood is reversed. This was formerly the right branch of the umbilical vein, its blood passing from left to right. It now becomes the left branch of the portal vein; and its blood passes from right to left, for distribution to the capillary vessels of the left lobe.

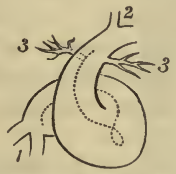
According to Guy, the umbilical vein, in man, is completely closed at the end of the fifth day after birth.

The Heart, and Ductus Arteriosus.—When the embryonic circulation is first established, the heart is a straight tubular canal (Fig. 246), receiving the veins at its lower extremity and giving off an arterial trunk at its upper extremity. It soon afterward becomes bent in a sharp curve (Fig. 247), which brings its venous and arterial extremities nearer the same level; but in such a way that its venous portion is situated behind, and its arterial portion in front. It has still a single, undivided cavity; and the blood passes through it in a continuous stream, turning upon itself at the point of curvature and emerging by the arterial orifice.

Fig. 246.

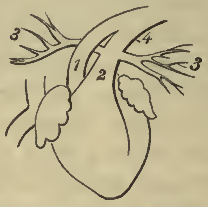
Earliest form of the Fœtal Heart. — 1. Venous extremity. 2. Arterial extremity.

Fig. 247.



Fœtal Heart, bent upon itself.—1. Venous extremity. 2. Arterial extremity.

Fig. 248.



Fœtal Heart still farther developed.—1. Aorta. 2. Pulmonary artery. 3, 3. Pulmonary branches. 4. Ductus arteriosus.

Subsequently the venous extremity of the heart shows a longitudinal furrow which divides its originally single cavity into two secondary compartments, placed side by side. These compartments become the right and left auricles; and they are furthermore separated, by transverse constrictions, from the curved portion of the heart, which is to form the ventricles. The cavities of the two ventricles become separated from each other by the growth of a septum, which begins at the most prominent part of the curvature or apex of the organ, and gradually extends toward its base. When the interventricular septum is completely formed, its situation is indicated by a corresponding furrow on the external surface of the organ.

The primitive arterial trunk, springing from the upper extremity of the heart, has already been divided, by a longitudinal furrow, into two secondary trunks, lying side by side and nearly parallel with each other

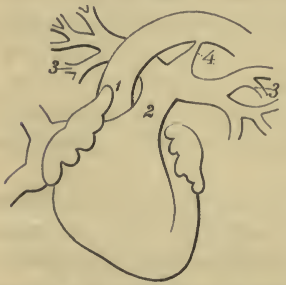
(Fig. 248). One of these secondary trunks becomes the commencement of the aorta, the other the pulmonary artery; and the relation of the furrow between them to the interventricular septum is such that the aorta communicates with the left ventricle, and the pulmonary artery with the right.

But the pulmonary artery, beside supplying small branches on each side to the lungs, also furnishes a large branch of communication to the arch of the aorta beyond. This branch is so voluminous that it appears to be the main continuation of the pulmonary trunk. It forms, accordingly, an open canal or duct between the two principal arteries nearest the heart, and is known by the name of the *Ductus arteriosus.*

The ductus arteriosus is at first almost as large as the pulmonary trunk; and nearly the whole of the blood from the right ventricle passes through it to the aorta, only an insignificant quantity being distributed to the lungs. But as the lungs become developed, the pulmonary branches increase in size, though not sufficiently to receive all the blood of the pulmonary trunk. At the termination of fœtal life, in man, the ductus arteriosus is about as large as either of the pulmonary branches; and a considerable portion of the blood, therefore, coming from the right ventricle, still passes onward to the aorta without being distributed to the lungs.

But at birth, when the lungs begin the performance of respiration, they receive a greater supply of blood. The right and left pulmonary branches enlarge, so as to become the principal divisions of the pulmonary trunk (Fig. 249). The ductus arteriosus at the same time diminishes in size, and is soon obliterated. It remains, in the adult, as an impervious cord, running from the bifurcation of the pulmonary artery to the under side of the arch of the aorta. The obliteration of its cavity is usually completed by the tenth week after birth. (Guy.)

Fig. 249.

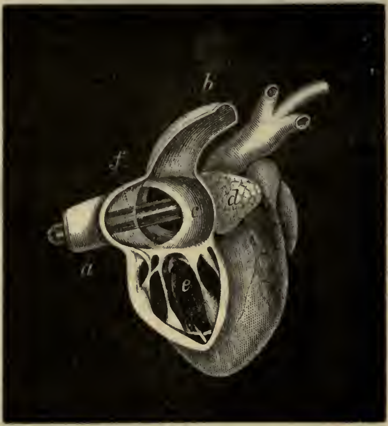


Heart of Infant, showing the disappearance of the arterial duct after birth.—1. Aorta. 2. Pulmonary artery. 3, 3. Pulmonary branches. 4. Ductus arteriosus becoming obliterated.

The interventricular septum, by which the two ventricles are separated from each other, is formed at an early date; but the interauricular septum remains for a long time incomplete, being perforated by an oval-shaped opening, the *foramen ovale,* which allows a free passage from the right auricle to the left. The existence of the foramen ovale and ductus arteriosus gives rise to a peculiar crossing of the streams of blood in the heart, characteristic of fœtal life, as follows:

In the fœtus the two venæ cavæ open into the right auricle on different planes and in different directions. While the superior vena cava is situated anteriorly, and is directed downward and forward, the inferior is situated posteriorly, and joins the auricle in a direction from right to left. A nearly vertical curtain or valve projects at the same time behind the orifice of the superior vena cava and in front of the orifice of the inferior. This curtain is formed by the incomplete septum of the auricles, which terminates inferiorly and toward the right in a crescentic border, at the foramen ovale. The stream of blood, coming from the superior vena cava, falls in front of this curtain, and passes downward, through the auriculo-ventricular orifice, into the right ventricle. But the inferior vena cava, owing to its posterior and transverse position, opens, properly speaking, not into the right auricle, but into the left. Its stream of blood, falling behind the above-mentioned curtain, passes across, through the foramen ovale, into the left auricle. This direction of the current from the inferior vena cava is further secured by a second membranous partition, which exists at this period, termed the *Eustachian valve.* This valve, which is very thin and transparent (Fig. 250, *f*), is attached in front of the orifice of the inferior vena cava, and terminates by a crescentic edge toward the left; thus standing between the cavities of the inferior vena cava and right auricle. A bougie, placed in the inferior vena cava, as in Fig. 250, lies behind the Eustachian valve, and passes through the foramen ovale, into the left auricle.

FIG. 250.



HEART OF THE HUMAN FŒTUS, at the end of the sixth month.—*a.* Inferior vena cava. *b.* Superior vena cava. *c.* Cavity of the right auricle, laid open from the front. *d.* Appendix auricularis. *e.* Cavity of the right ventricle. *f.* Eustachian valve. The bougie, placed in the inferior vena cava, can be seen passing behind the Eustachian valve, just below the point *f*, then crossing, behind the right auricle, through the foramen ovale, to the left side of the heart.

The two streams of blood, therefore, coming from the superior and inferior venæ cavæ, cross each other on entering the heart. Owing to the position of the two veins and their adjacent valves, the stream coming from the superior vena cava enters the right auricle, while that from the inferior passes transversely into the left.

The relations of the aorta, pulmonary artery, and ductus arteriosus at this time are such that the arteria innominata, the left carotid and left subclavian arteries are given off from the arch of the aorta, before the junction of the ductus arteriosus; and thus the blood-currents of the two venæ cavæ are distributed, after leaving the ventricles, to different parts of the body (Fig. 251). The blood of the superior vena cava passes through the right auricle into the right ventricle, thence through the pulmonary artery and ductus arteriosus, to the thoracic aorta; while the blood of the inferior vena cava, entering the left auricle and left ventricle, passes into the arch of the aorta, and is distributed to the head and upper limbs. The two streams, therefore, in passing through the heart, cross each other both behind and in front. The venous blood, returning from the head and upper limbs by the superior vena cava, passes, through the thoracic and abdominal aorta and the umbilical arteries, to the lower part of the body, and to the placenta; while that returning from the placenta, by the inferior vena cava, is distributed to the head and upper limbs, through the vessels given off from the arch of the aorta.

Fig. 251.

Diagram of the Circulation through the Fœtal Heart.—*a*. Superior vena cava. *b*. Inferior vena cava. *c*, *c*, *c*, *c*. Arch of the aorta and its branches. *d*. Pulmonary artery.

This division of the streams of blood, during a certain period of fœtal life, is so complete that Reid,* on injecting the inferior vena cava with red, and the superior with yellow, in a human fœtus of seven months, found that the red injection had passed through the foramen ovale into the left auricle and ventricle and the arch of the aorta, and had filled the vessels of the head and upper limbs; while the yellow had passed into the right ventricle, pulmonary artery, ductus arteriosus, and thoracic aorta, with only a slight admixture of red at the posterior part of the right auricle. All the branches of the thoracic and abdominal aorta were filled with yellow, while the whole of the red had passed to the upper part of the body.

We have several times repeated this experiment on the fœtal pig, when about one-half or three-quarters grown, first washing out the heart and large vessels with a watery injection, to prevent their obstruction by coagulated blood. The injections used were blue for the superior vena cava, and yellow for the inferior. The two syringes were managed, at the same time, by the right and left hands; their nozzles being held in place by an assistant. When the points of the syringes were introduced into the veins at equal distances from the heart, and the two injections made with equal rapidity, it was found that at least nineteen-twentieths of the yellow injection had passed into the left auricle, and nineteen-twentieths of the blue into the right. The pulmonary artery and ductus arteriosus contained a similar proportion of blue, and the arch of the aorta of yellow. In the thoracic aorta, however, there was always an admixture of the two colors, generally in about equal proportions. This may be owing to the smaller size of the

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* Edinburgh Medical and Surgical Journal, 1835, vol. xliii., p. 11.

head and upper extremities in the pig, as compared with the human fœtus, which would prevent their receiving all the blood coming from the left ventricle; or to some difference in the manipulation of these experiments, in which it is not always easy to imitate the force and rapidity of the blood currents in the living body. The results, however, leave no doubt that, up to an advanced stage of fœtal life, most of the blood from the inferior vena cava passes through the foramen ovale into the left side of the heart; while most of that coming from the head and upper limbs passes into the right side of the heart, and thence outward by the pulmonary trunk and ductus arteriosus. Toward the latter periods of gestation, this division of the venous currents becomes less complete, owing to the following causes:

First, the two pulmonary arteries, as well as the pulmonary veins, enlarge in proportion to the increased size of the lungs; and a greater quantity of blood from the right ventricle, instead of passing through the ductus arteriosus, is distributed to the lungs, and, returning thence to the left auricle and ventricle, joins the stream passing out by the arch of the aorta.

Secondly, the Eustachian valve diminishes in size. This valve, which is very large at the end of the sixth month, subsequently becomes atrophied, and at the end of gestation is too small to exert any influence on the current of the blood. Thus, the cavity of the inferior vena cava, at its upper extremity, ceases to be separated from that of the right auricle.

Thirdly, the foramen ovale becomes partially closed by a valvular partition growing from behind forward. This valve, which begins to be formed at a very early period, is the *valve of the foramen ovale.* It is a thin, fibrous sheet, attached to the posterior surface of the auricular cavity a little to the left of the foramen ovale, and projecting by its free border into the left auricle. It accordingly does not interfere at this time with the flow of blood from right to left, and only prevents regurgitation from left to right.

But as gestation advances, while the heart continues to enlarge, and its cavities expand in every direction, the fibrous bundles, forming the valve do not elongate in proportion. The valve, accordingly, becomes drawn down more closely across the foramen ovale. It thus comes in contact with the inter-auricular septum, and unites with its substance; the adhesion taking place first at its lower and posterior portion, and extending gradually upward and forward, so that the passage from the right auricle to the left becomes more oblique.

At the same time the inferior vena cava alters its position. This vessel, which at first looked transversely toward the foramen ovale, turns partially forward; and as the Eustachian valve has now nearly disappeared, some of the blood from the inferior vena cava enters the right auricle, while the remainder still passes through the foramen ovale.

At birth a change takes place, by which the foramen ovale is completely occluded, and all the blood coming through the inferior vena cava is turned into the right auricle.

This change depends on the commencement of respiration, by which the quantity of blood passing through the lungs is largely increased. The left auricle, thus supplied to its full capacity with blood returning from the lungs, no longer admits the entrance of a further quantity through the foramen ovale; and the valve of the foramen, pressed backward against the septum, becomes after a time adherent throughout, and obliterates the opening. The cutting off of the placental circulation also diminishes the volume of blood in the inferior vena cava. It is evident that the same quantity which previously returned from the placenta by the inferior vena cava on the right side of the inter-auricular septum, now returns from the lungs, by the pulmonary veins, on the left side of the same septum; and, the pressure being thus equalized in the right and left auricles, there is no mixture of the blood between the two.

FIG. 252.

DIAGRAM OF THE ADULT CIRCULATION THROUGH THE HEART.—*a, a.* Superior and inferior venæ cavæ. *b.* Right ventricle. *c.* Pulmonary artery, dividing into right and left branches. *d.* Pulmonary vein. *e.* Left ventricle. *f.* Aorta.

The fœtal circulation is then replaced by the adult circulation, represented in Fig. 252.

That portion of the inter-auricular septum, originally occupied by the foramen ovale, is accordingly formed, after birth, by the valve of this foramen, which has become adherent to its edges. The septum in the adult heart is thinner at this spot than elsewhere; and presents, on its right side, an oval depression, termed the *fossa ovalis,* indicating the site of the original foramen ovale. The fossa ovalis is surrounded by a slightly raised ring, the *annulus ovalis,* representing the edge of the original inter-auricular septum.

The foramen ovale is sometimes completely obliterated within a few days after birth, but often continues partially pervious for several weeks or months; and it is not unfrequent to find a small aperture remaining in adult life. In these instances, although the consolidation of the inter-auricular septum is incomplete, yet no admixture of blood takes place between the two sides of the heart. The oblique direction of the passage and its valvular arrangement prevent any regurgitation from left to right; and the complete filling of the left auricle with blood from the lungs is a sufficient obstacle to the entrance of venous blood from the right.

CHAPTER XVII.

DEVELOPMENT OF THE BODY AFTER BIRTH.

THE newly-born infant is still far from a condition of complete development. The changes through which it has passed in fœtal life are followed by others during infancy, childhood, and adolescence. The anatomy of the organs, their physiological functions, and even the morbid derangements to which they are subject, continue to undergo progressive alterations throughout the whole course of subsequent life. The history of development extends, properly speaking, from the earliest organization of the embryonic tissues to the complete formation of the adult body. The period of birth is only a single epoch in a long series of changes, some of which have preceded, while many others are to follow.

The weight of the newly-born infant is about seven pounds. The middle point of the body is nearly at the umbilicus, the head and upper limbs being still large, in proportion to the lower limbs and pelvis. The abdomen is larger and the chest smaller, in proportion, than in the adult. The lower limbs are still partially curved inward, so that the soles of the feet look obliquely toward each other, instead of being directed horizontally downward, as at a subsequent period. The arms and legs are curled forward over the chest and abdomen, and all the joints are in a semi-flexed position.

The process of respiration is imperfectly performed for some time after birth. The expansion of the pulmonary vesicles, and the accompanying changes in the circulation at birth, far from being instantaneous, are more or less gradual, requiring an interval of several days for their completion. Respiration seems to be accomplished, during this period, to a considerable extent through the skin, which is soft. vascular, and ruddy. The animal heat is less actively generated than in the adult, and requires to be sustained by careful protection, and by contact with the body of the mother. The young infant sleeps during the greater part of the time; and when awake exhibits but few manifestations of intelligence or perception. The special senses are comparatively inexcitable, and even consciousness seems present only to a limited extent. Voluntary motion and sensation are nearly absent; and the almost constant irregular movements of the limbs, observable at this time, are mainly automatic. Nearly all the nervous phenomena presented by the newly-born infant, are of a similar nature. The motions of its hands and feet, the act of suckling, and even its cries and the contortions of its face, are reflex in origin, and do not indicate any active volition, or distinct perception of external objects. There is but little nervous connection with the external world, and the system is occupied almost exclusively with the functions of nutrition and respiration.

The difference in organization between the newly-born infant and the adult is represented, to some extent, in the following list, which gives the relative weight of the most important organs at the period of birth and in adult age; the weight of the entire body being reckoned, in each case, as 1000. The relative weight of the adult organs is calculated from the estimates of Cruveilhier, Solly, and Wilson, that of the organs in the fœtus at term from our own observations:

	Fœtus at term.	Adult.
Weight of the entire body . . .	1000.00	1000.00
" " encephalon . . .	148.00	23.00
" " liver	37.00	29.00
" " heart	7.77	4.17
" " kidneys	6.00	4.00
" " supra-renal capsules .	1.63	0.13
" " thyroid gland . .	0.60	0.51
" " thymus gland . .	3.00	0.00

It appears that most of the internal organs diminish in relative size after birth, owing principally to the increased development of the osseous and muscular systems, both of which are very imperfect throughout intra-uterine life, but come into activity during childhood and youth.

The remains of the umbilical cord begin to wither within twenty-four hours after birth, and become completely desiccated by about the third day. A superficial ulceration then takes place at its point of attachment, and it is thrown off within the first week. After separation of the cord, the umbilicus becomes completely cicatrized by the tenth or twelfth day. (Guy.)

An exfoliation and renovation of the cuticle takes place over the whole body soon after birth. According to Kölliker, the eyelashes, and probably all the hairs of the body and head, are thrown off and replaced by others within the first year.

The teeth in the newly-born infant are but partially developed, being still enclosed in their follicles and concealed beneath the gums. They are twenty in number, namely, two incisor, one canine, and two molar teeth on each side of each jaw. At birth there is a thin layer of dentine and enamel covering their upper surfaces, but the body and fangs of the tooth are formed subsequently by progressive elongation and ossification of the tooth-pulp. The fully formed teeth emerge from the gums in the following order: The central incisors in the seventh month after birth; the lateral incisors in the eighth month; the anterior molars at the end of the first year; the canines at a year and a half; and the second molars at two years (Kölliker). The eruption of the teeth in the lower jaw generally precedes by a short time that of the corresponding teeth in the upper jaw.

During the seventh year a change begins to take place by which the first set of teeth are replaced by the second or permanent set. The anterior permanent molar tooth first shows itself just behind the posterior temporary molar, on each side. This happens at about six and a half years after birth. At the end of the seventh year the middle incisors are thrown off and replaced by corresponding permanent teeth, of larger size. At the eighth year a similar exchange takes place in the lateral incisors. In the ninth and tenth years, the anterior and second molars are replaced by the anterior and second permanent bicuspid teeth. In the twelfth year, the canine teeth are changed. In the thirteenth year the second permanent molars show themselves; and from the seventeenth to the twenty-first year, the third molars, or "wisdom teeth," emerge from the gums, at the extremities of the dental arch. (Wilson). The jaw, therefore, in the adult condition, contains three teeth on each side more than in childhood, making in all thirty-two permanent teeth; namely, on each side, above and below, two incisors, one canine, two bicuspids, and three permanent molars.

The generative apparatus, which is inactive at birth, begins its functional activity from the fifteenth to the twentieth year. The general configuration of the body alters at this period, and the distinction between the sexes becomes more marked. The beard is developed in the male; and in the female the breasts assume the size and form characteristic of puberty. The voice, which is shrill and sharp in infancy and childhood, becomes deeper in tone, and the countenance assumes a more sedate expression. After this period, the muscular system increases still farther in size and strength, and the consolidation of the skeleton also continues; the bony union of its various parts not being entirely accomplished until the twenty-fifth or thirtieth year. Finally, all the organs of the body arrive at the adult condition, and the entire process of development is then complete.

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